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Biology and Silviculture of Northern Red Oak in the North Central Region: A Synopsis

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FOREWORD

In 1990 several North Central Forest Experiment Station scientists were asked to contribute papers on basic biology and silviculture to a monograph on the northern red oak sponsored by the National Institute of Agronomic Research (INRA) in France. After much discussion, INRA decided to publish the monograph articles exclusively in French. The publication process of that monograph was much delayed due to translation and administrative problems. However, recently a handsome handbound monograph was published entitled "Le Chene Rouge d' Amerique" by Timbal *et al.* (1994). Due to the fact that INRA's publication was delayed several years and that many of our research clients are not competent in French, we asked and received permission from INRA to update and publish a synopsis of our scientists' contributions to their monograph in English in this North Central Forest Experiment Station publication. We would like to acknowledge the generous cooperation of the monograph editors Dr.'s J. Timbal and A. Kremer, in this regard.

Biology and Silviculture of Northern Red Oak in the North Central Region: a Synopsis

J.G. Isebrands and R.E. Dickson

INTRODUCTION

Northern red oak (*Quercus rubra* L.) is one of the most widespread and valuable tree species in Eastern North America. It is highly valued for wildlife food and habitat, timber and veneer, aesthetics, and as an urban tree. Northern red oak is also considered an important component for maintaining biodiversity in eastern forest ecosystems. In addition, it is becoming increasingly important as an exotic forest species in western Europe, particularly in France.

Unfortunately, northern red oak is difficult to regenerate by either natural or artificial methods. The difficulty in regeneration is particularly disturbing in that northern red oak stands are currently being heavily logged by private landowners throughout the East because of its high oak lumber value, and are being heavily attacked by pests, including gypsy moth (*Lymantria dispar* L.) and oak wilt [Ceratocystis sogacearum (Bretz) Hunt.].

The difficulty in regenerating northern red oak has led to numerous research efforts, literature reviews, and symposia aimed at improving silvicultural strategies and filling gaps in our scientific knowledge about oak regeneration. Despite these efforts, many unanswered questions remain about how oaks regenerated in the past and how they can best be regenerated in the future. Furthermore, for a species of such importance, surprisingly little is known about the basic biology of northern red oak including shoot and root growth patterns, flowering, carbon assimilation and allocation, and nutrition. We believe that more basic scientific information, if available, could be used to develop better natural and artificial regeneration strategies.

This monograph includes four review papers on the biology and silviculture of northern red oak. The first paper outlines what is known about the episodic shoot growth patterns in northern red oak, although the mechanisms controlling the flushing patterns and frequent dieback of shoots observed in the field are still unknown. The second paper reviews flowering, fertilization, and acorn production patterns in northern red oak and how they relate to shoot growth and environmental factors. The third paper focuses on carbon fixation and allocation patterns in northern red oak, which largely depend on the specific stage of shoot growth and timing in response to various silvicultural treatments and environmental stresses. Moreover, in mature trees, carbon allocation patterns are strongly influenced by flowering and acorn production. In fact, during heavy flowering and fruiting years, a significant portion of the total carbon budget is used in the reproductive process. The fourth paper reviews the current knowledge on the silviculture of northern red oak. Knowledge of basic biology such as carbon allocation patterns is important silviculturally because stem and root growth depends upon current carbon assimilates. Moreover, silvicultural practices can be designed to take advantage of what we know about physiological processes and growth patterns. For example, shelterwood cuts can be used to create understory conditions of light and soil moisture to ensure growth of seedlings and advanced regeneration. Also, nursery practices such as undercutting, fertilization, and irrigation can be timed to take maximum advantage of the cyclic relations between shoot growth and root growth. We hope that our synopsis of the latest biological and silvicultural information will fill an important knowledge gap and lead to improved regeneration of future oak forest ecosystems in our region.

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Height Growth and Episodic Flushing in Northern Red Oak

Richard E. Dickson

INTRODUCTION

Different tree species have different seasonal patterns of shoot growth. Such patterns have long attracted research interest, and this research has been extensively reviewed (Romberger 1963, Kozlowski 1964, Rudolph 1964, Borchert 1991). Shoot growth patterns can be broadly classified as determinate, semi-determinate, or indeterminate (fig. 1). These classifications are not clear-cut but involve considerable overlap. In all three classifications, the first flush of growth involves expansion of preformed stem units (primordia-node-internode) contained in the overwintering bud. Trees with determinate growth habit exhibit only a single growth flush in the spring, which involves the elongation and maturation of these preformed stem units in the bud. Trees with semi-determinate growth habit exhibit recurrent, cyclic, or episodic flushes of growth during the growing season. Trees with indeterminate growth habit produce individual leaves at regular intervals during the growing season. However, both determinate and indeterminate plants exhibit rhythmic growth cycles during shoot expansion that are not obvious without frequent measurements of shoot growth (Borchert 1978, Drew 1982).

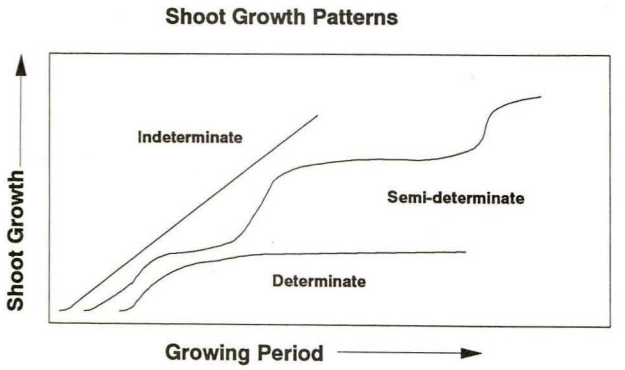

Figure 1.—*Three inherent annual shoot growth patterns common in forest tree species (redrawn from Dickson 1991).*

In plants with true or "classical" episodic flushing growth habit, shoot growth is controlled by endogenous factors (Borchert 1975, 1991). Under suitable environmental conditions, a true growth flush involves expansion of the resting bud, expansion and maturation of new stem and leaves, formation of a new resting bud, and a rest period in which no new leaf or stem elongation takes place. These episodic growth flushes will continue as long as environmental conditions are favorable. Episodic growth is common in many tropical trees (Halle and Martin 1968, Greathouse *et al.* 1971, Borchert 1978, Maillard *et al.* 1989), in some conifers (Rudolph 1964, Kremer and Larson 1983, Hendry and Gholz 1986, Von Wuhlisch and Muhs 1987, O'Reilly and Owens 1989), and in some northern hardwoods (Borchert 1975, Reich *et al.* 1980, Hanson *et al.* 1986). Northern red oak is a good example of a hardwood with episodic flushing growth habit. It is my objective in this paper to examine episodic growth in northern red oak, to compare this growth habit to more intensively studied tropical trees, to discuss some of the proposed control mechanisms, and to point out major gaps in our knowledge of episodic growth and some potential research required to fill in these gaps.

Most of our work with northern red oak (*Quercus rubra* L.) has involved one- to four-flush potted seedlings or nursery stock. However, there is no reason to believe that the basic mechanisms controlling episodic growth differ between small and large trees, between different tree species, or between trees of temperate or tropical climates. Information on the basic mechanisms that control episodic flushing in northern red oak could be applied to other flushing species. In addition, such information could lead to improved nursery practices and improved silvicultural practices for establishment and early growth of both natural and artificial regeneration.

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STEM AND LEAF GROWTH OF NORTHERN RED OAK

The growth potential of northern red oak is excellent, although seldom obtained in the field. In growth room or controlled environments with adequate water and fertilization, seedlings will continue to flush until the roots become restricted by the pots (pot-bound). Under our controlled environment growing conditions at Rhinelander, Wisconsin, three-flush seedlings 80 cm tall are obtained within 60 days after emergence from the potting mix (fig. 2). Six-flush seedlings up to 2 m tall can be produced in the growth rooms before the seedlings become pot-bound and stop episodic flushing. During a growth flush, internode elongation begins first and is largely completed before the leaves begin to expand (fig. 2) (Hanson *et al.* 1986). Similar expansion of stems and then leaves was found in *Hevea* during a flush (Halle and Martin 1968). In contrast, stem and leaves of *Theobroma* expand at about the same time (Greathouse *et al.* 1971). A typical pattern of stem, internode, and leaf development is shown by measurements taken during expansion of the second flush of red oak (fig. 3). Both internodes and leaves, when measured acropetally, increase then decrease progressively in size during flush development. The last internodes and the last leaf of a flush are often much smaller than previous stem units (leaf-node-internode) indicating growth inhibition during the last phase of the flush. The growth patterns seen here (fig. 3) most likely result from endogenous control mechanisms because environmental conditions did not change during the flush.

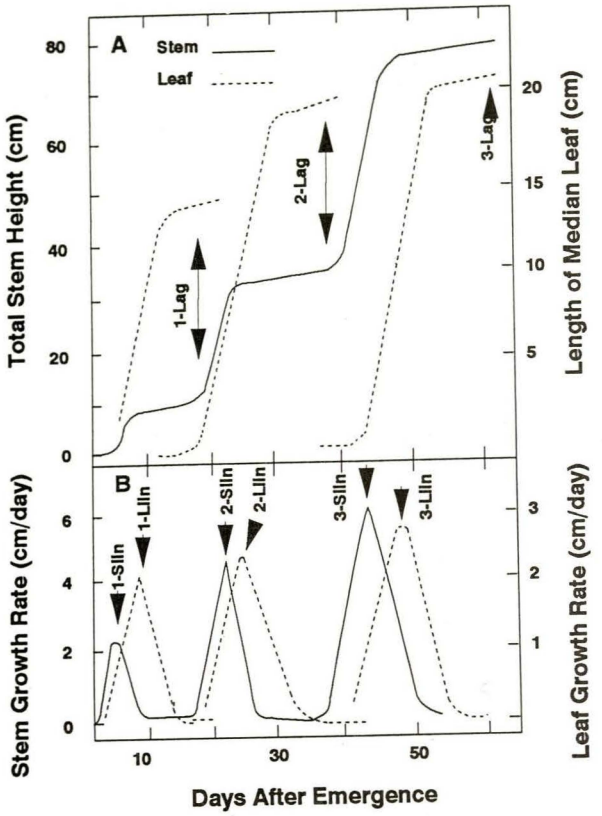

Figure 2.—*Episodic shoot growth pattern of a three-flush northern red oak* (Quercus rubra *L.) seedling following epicotyl emergence from the soil. (A) Total stem and leaf length. (B) Rate of stem and leaf elongation. Leaf growth is based on the median leaf of each flush. Growth curves are smoothed curves based on data from 12 seedlings. Arrows indicate specific developmental stages based on the* Quercus *morphological index (QMI). The QMI defines three growth stages in each flush (e.g., in the first flush, 1-stem linear, 1-leaf linear, and 1-lag) redrawn from Hanson* et al. *1986).*

POTENTIAL ENDOGENOUS CONTROL MECHANISMS

Endogenous mechanisms within the plant control the rhythmic growth or episodic flushing of oak and other species of trees grown under constant environmental conditions or under fluctuating environmental conditions still conducive to growth. At the end of a growth flush, leaf expansion stops and a dormant (resting) bud is initiated. This bud is initiated and held in a dormant state by endogenous control mechanisms (Greathouse *et al.* 1971, Mialoundama *et al.* 1984). The dormant state is apparently induced by a biochemical signal originating in some other part of the plant and could be termed paradormancy (Lang *et al.* 1987). The various states of dormancy and related terminology have been extensively discussed in the past and will not be repeated here (Romberger 1963, Levins 1969, Perry 1971, Champagnat 1983, Lang *et al.* 1987).

The development of the resting bud is much different from the development of a winter dormant bud. Although we did not study it in detail, the resting bud in red oak is much smaller than the winter bud and covered with stipules that do not expand to form bud scales. When the next flush expands, the basal 1 to 5 internodes elongate very little, and have stiples present but no leaves (Hanson *et al.* 1986).

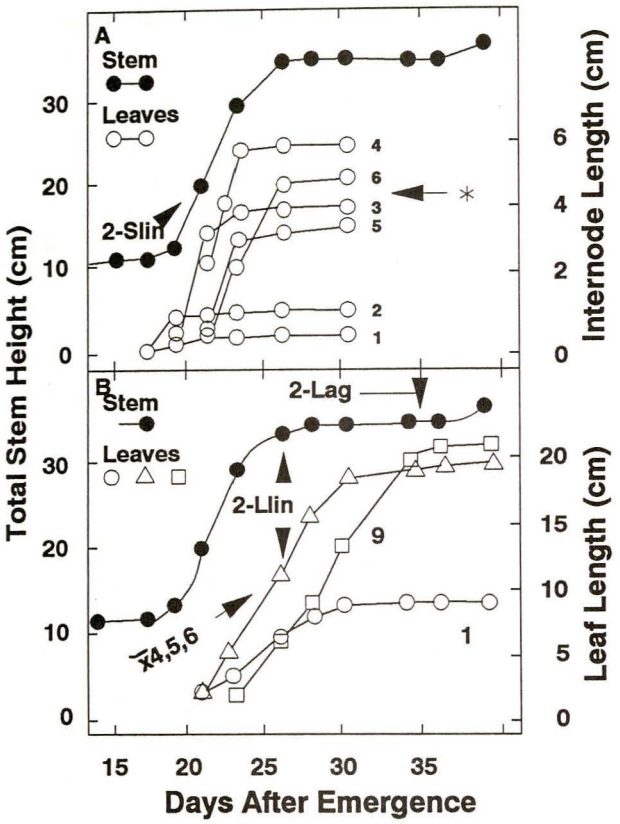

Figure 3.—*Individual internode and leaf growth patterns in the second flush of a northern red oak* (Quercus rubra *L.) seedling. (A) Individual internodes and total stem height. Internodes 7 to 11 are omitted for clarity. Internode 3 subtends the first leaf on the second flush. Individual internode lengths normally increase then decrease from base to top of a flush. (B) Individual leaves and total stem height. Curves are drawn only for the lowest leaf (leaf 1); median leaves 4, 5, and 6; and the uppermost leaf (leaf 9). Arrows indicate different QMI stages for the second flush.*

Similar growth patterns were found for *Theobroma* (Greathouse *et al.* 1971, Vogel 1975) and *Hevea* (Halle and Martin 1968, Borchert 1991). We do not know why these basal leaves do not develop. Perhaps these leaf primordia (last formed on the current flush or first formed on the next flush?) that receive the rest signal abort as was found for cottonwood (*Populus deltoides*) (Goffinet and Larson 1981). The exact timing of primordia initiation in respect to the flush cycle requires further careful study. Barnola *et al.* (1986) reported that primordia initiation was continuous over the entire flush cycle. Their figure 2, however, indicates an increased rate of initiation during the flush. Rhythmic initiation of primordia in association with leaf and stem expansion of the new flush was found in *Theobroma* (Greathouse *et al.* 1971) and *Gnetum* (Mialoundama *et al.* 1984). In contrast, Purohit and Nanda (1968) reported that primordia were initiated during the lag phase of the vegetative flushes in *Callistemon*.

Although several hypotheses have been presented, the endogenous control mechanisms that regulate leaf and internode expansion and primordia initiation are unknown. Different hormones, water stress, carbohydrate concentrations and interactions between these factors have all been implicated. Some researchers believe that water stress, initiated in the shoot by a decreasing rate of root growth (Borchert 1975, 1978, 1991) or by competition between leaves and the developing apex for available water (Halle and Martin 1968, McIntyre 1987), induces bud rest and episodic growth. Others have implicated abscisic acid (ABA) or the interactions of ABA and water stress (Orchard *et al.* 1980, 1981; Abo-Hamed *et al.* 1981, 1983). Still others believe that varying concentrations of cytokinins are important in slowing leaf development or initiating bud break (Wareing 1980, Orchard *et al.* 1981, Carmi and Van Staden 1983). The best scenario seems to be that during a flush, photosynthate movement to roots decreases, root growth decreases, water stress and ABA concentrations increase, cytokinin concentrations and/or translocation decrease, primordia development decreases, leaf growth decreases, and buds set (Orchard *et al.* 1981, Alatou *et al.* 1989). Because it is very difficult to separate the effects of each of these factors and their interactions, the mechanism of endogenous control of episodic flushing is far from clear (Wareing 1980, Little and Wareing 1981, Zeevaart and Creelman 1988). What is clear is that a functional equilibrium between shoots and roots (in relative growth rates, nutrient uptake, carbohydrate allocation, hormone production and transport, and water movement) must be maintained if the episodic growth cycles are maintained.

SHOOT-ROOT INTERACTIONS

There is no question that relative shoot and root growth is closely controlled by metabolic interactions between the shoot and roots. This functional equilibrium has been recognized for a long time and has been extensively studied (Lyr

and Hoffmann 1967, Brouwer 1983, Lambers 1983, Schulze 1983); it can be viewed simply as changes in carbon allocation (de Wit and Penning de Vries 1983) or as a much more complex system of carbon, mineral nutrients, and hormonal interactions (Carmi 1986, Zhang and Davies 1989).

In trees with episodic shoot growth, both constant (Halle and Martin 1968) and episodic (Vogel 1975) root growth has been found. In our research with northern red oak, root growth rates are constant as long as the cotyledons are attached. Apparently nutrients from the cotyledons can maintain root growth during episodic growth of the shoot (Hanson 1986). Similar continuous root growth has been found in other oak species (Lavarenne 1968, Belgrand *et al.* 1987). In addition, we have found that in older seedlings and in seedlings with detached cotyledons, root growth is also episodic and out of phase with the shoot. Similar results have been presented by others (Hoffmann 1967, Reich *et al.* 1980, Nour and Riedacker 1984). It is difficult to understand how roots growing at a constant rate can induce episodic growth in shoots.

Borchert (1991) has proposed that the increasing leaf area produced during a flush increases water stress in the shoot, which initiates the lag phase in shoot growth. Removing whole or parts of new leaves to maintain a smaller leaf area will often increase flushing rate or initiate continuous shoot growth, thus substantiating this hypothesis (Halle and Martin 1968, Borchert 1975, Vogel 1975, Hilton *et al.* 1987). The differential translocation of nutrients and hormones, however, cannot be ruled out. During a flush when the growth of new leaves takes place, almost no photosynthate from mature leaves is translocated to the root system (Dickson 1989, Isebrands *et al.* 1994). During the lag phase when new leaves are fully expanded, more than 90 percent of current photosynthate is translocated to the root system. This current photosynthate may be important in cycling nutrients and hormones from roots to shoots and in initiating bud break and a new episodic flush of growth. This cycling of carbohydrates to roots and of nutrients (particularly nitrogen) and hormones (e.g., cytokinins) back to shoots would be even more important when both shoots and roots have episodic and out of phase growth patterns (Sleigh *et al.* 1984, Dickson and Isebrands 1991).

EPISODIC GROWTH UNDER NATURAL CONDITIONS

Most studies on episodic growth were conducted in controlled environments with small seedlings. Environmental stress, however, may severely modify these endogenous growth patterns (Gaertner 1964, Lavender 1980). In field situations, where multiple stresses are often present, oak seedlings commonly make only one spring flush of growth (Reich *et al.* 1980). Light, moisture, temperature, and nitrogen stresses may affect episodic flushing. The response of different species probably differs widely with any particular stress, and the response to multiple stresses may differ from that obtained with a single stress if other factors are near optimum. Northern red oak, when grown in our controlled environment with adequate nutrients and water, will continue to flush until it becomes pot-bound. Low light intensity (300 uE $m^{-2}s^{-1}$, about 20 percent full sun) or short days (8 hours of light) have little effect on this endogenous growth rhythm. When plants were grown in a growth room, in a glasshouse, or outside with adequate water and nutrients, flushing was again continuous, but the flushing interval increased in the higher stress situations. For example, the interval for one lag to two lag increased from 17 to 30 to 36 days for the growth room, greenhouse, and outside plants, respectively.

Most studies of episodic growth have been conducted with small seedlings. Such plants have relatively simple shoot and root systems, strong apical dominance, and many other juvenile characteristics. Such plants may grow continuously (indeterminate leaf production) and produce up to 30 or 40 leaves before resuming episodic growth. Others will flush repeatedly until inhibited by pot size or other environmental conditions. Such repeated episodic growth is largely restricted to small seedlings and juvenile plants and not commonly found in large trees. Stump sprouts, however, are an exception. Because such plants have a large root system and large amounts of stored nutrients, shoot growth may be continuous or have several large episodic flushes during the growing season (Borchert 1978, Johnson 1979, Reich *et al.* 1980, Cobb *et al.* 1985, Tworkoski *et al.* 1990, Harmer 1992). Large, mature trees, however, commonly have only one flush of leaf growth early in the growing season. As trees

grow larger, the number of growing shoots or branches increases and the complexity of the shoot system increases (Borchert 1976). This leads to a large positional differentiation among individual branches and shoots (terminal vs. lateral, long vs. short shoots, upper vs. lower crown). There is no evidence that large trees have different or better control systems than small trees (Borchert 1978). Therefore, the short duration of active growth and the single flush common in large trees must result from a correlative inhibition of growth among different shoots in the crown and feedback inhibition between shoots and roots. The feedback cycles are fairly short in small seedlings (e.g., 15 to 20 days between one-lag and two-lag seedlings (fig. 2), probably because of the smaller distance involved in transport of growth controlling substances and the quicker response time of the seedling. In large trees, this feedback inhibition cycle between shoots and roots may be so long that changing environmental conditions of late summer (increased temperature and decreased soil moisture) may overtake the tree and inhibit further shoot growth even though a favorable shoot/root ratio has been reestablished. Defoliation or severe pruning of a large tree may remove the correlative inhibition among shoots and decrease the shoot/root ratio thus leading to additional flushing.

ADDITIONAL AREAS FOR RESEARCH

Hypothesis—Episodic growth is the result of genetic factors that provide a mechanism to control shoot/root ratios. This mechanism enables the plant to respond to good environmental conditions with rapid flush cycles and height growth while maintaining a balanced shoot/root ratio. Under adverse conditions, flushing or top growth stops and photosynthate is allocated to root growth and storage, a conservative feature that gives the plant the ability to survive severe environmental stress and to grow on sites with less favorable environments. The physiological, biochemical, and perhaps biophysical mechanisms that control episodic growth and maintain this functional equilibrium between shoots and roots are important research areas that require our immediate attention.

In reviewing the literature on episodic growth for this paper, I found several areas in which additional research on basic mechanisms would be helpful. Four of these areas are particularly important: (1) Exact timing of primordia initiation, (2) Antecedent leaf developmental and metabolic state, (3) Shoot/root interactions and feedback systems, and (4) Carbon-nitrogen relations. The timing of primordia initiation in northern red oak is not known. Careful anatomical and morphological studies based on the *Quercus* morphological index (QMI) (Hanson *et al.* 1986) could determine the exact timing of initiation. The timing of primordia initiation is probably associated with specific developmental and metabolic stages of the antecedent leaves.

The antecedent leaf is an older leaf or leaves directly connected by vascular traces to other developing leaves and primordia. The antecedent leaf provides metabolites and perhaps hormones for primordia initiation and subsequent leaf development (Dickson and Shive 1982, Larson 1983, Dickson and Isebrands 1991). These antecedent leaves are the major receptors of environmental stimuli and thus exert considerable control over the development of the apex and primordia initiation. Information on the metabolic state (e.g., QMI stage) of the antecedent leaves during development of the new flush would be helpful for elucidating basic control mechanisms.

There is no question that shoot and root growth is controlled by multiple feedback systems. Understanding the complementary functions of shoots and roots is a prerequisite to explaining whole-plant development. This is especially true when trying to understand episodic growth. During the lag phase in northern red oak, more than 90 percent of the photosynthate translocated from maturing leaves is allocated to lower stem and the root system (Dickson 1991). This photosynthate is used in new root growth, storage, and more importantly, in recycling of amino acids, hormones, and other chemical compounds from roots to shoots in the xylem.

Related to the above three research areas is a lack of understanding about basic carbon and nitrogen interactions. Nitrogen is absorbed by the roots, reduced in the roots if absorbed as nitrate, converted to organic nitrogen compounds, and translocated in the xylem to shoots. Distribution within the shoot (leaves, stem, developing leaves, etc.) is largely controlled by the particular amino acid being translocated in the xylem because of differential

uptake from the transpiration stream in the stem (Vogelmann *et al.* 1985). Carbon translocated to the root system is required for energy to run these metabolic processes, and for the production of amino acids and organic acids for transport. Currently produced photosynthate translocated to roots may follow very different pathways compared to stored carbohydrate in roots (Dickson 1989). Thus, to understand and perhaps control episodic growth, detailed information is required on carbon-nitrogen interactions and differential metabolism in shoots and roots during a flush cycle.

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The Reproductive Biology of *Quercus*, with an Emphasis on *Q. rubra*

Robert A. Cecich

My original intent in this paper was to present a chronology of events for the reproductive biology of northern red oak (*Quercus rubra* L.) based on a review of the literature. However, because there is so little information available about northern red oak, results from studies of other species of *Quercus* will be included to provide some continuity. But this may lead some readers into a false sense of security about what we really know of the pathway from flowers to seed maturation in northern red oak.

There are two major subgenera in the North American oaks: lepidobalanus or the white oaks, and erythrobalanus or the red oaks. These two groups differ structurally and chemically. However, we will concern ourselves only with differences in the reproductive cycle. Simply put, the white oaks require only one growing season from the time of pollination to acorn maturation. The red oaks, however, require two growing seasons. Pollination occurs in the first season, and the ovule primordia remain as placentae or rudimentary bulges until the following growing season, when the ovules develop, fertilization is accomplished, and the acorns mature. These structures and processes will be the primary focus of this paper.

PISTILLATE FLOWERS

Acorns develop from fertilized pistillate (female) flowers. However, we know little about these flowers primarily because they exist in the crowns of tall trees (and, thus, are not easily studied). Also, because there has been little demand for oak breeding programs, there has been little desire to understand and manipulate the reproductive cycle. Our knowledge has almost exclusively been provided by botanists with an academic interest in studying a structure or process, and not by foresters with an interest in managing trees. Thus, the description of the flower must use specific botanical terminology. The developmental morphology of the unfertilized pistillate flower of *Q. rubra* was described by Langdon (1939) and Sattler (1973); their interpretations are combined in this part of the paper.

The pistillate flower originates as a stalk or inflorescence in the axil of a developing leaf primordium during the summer before pollination, and contains several bracts arranged spirally on its axis. After the inflorescence and bracts overwinter, floral apices differentiate in the axils of each of the lower, opposite bracts of the inflorescence, and then flatten and assume a three-cornered appearance as a result of growth occurring at their periphery. The individual flower, partially enclosed by a cupular involucre of imbricating scales, consists of a cup-shaped perianth tube, non-diverged from the walls of a three-celled ovary that bears three stigmatic styles. The involucre is first formed as a few separate primordia in the axils of the bracts located at the base of the floral apex. Three inner perianth members are initiated simultaneously between the outer perianth members, and all are then raised up on a common base as three gynoecial (carpel) primordia arise on the broad flat apex opposite the outer perianth members. The carpel primordia differentiate into the three stigmas.

In the first growing season, further ovary maturation occurs about 1 month after pollination. The young ovary becomes closed as a result of the appression of the three gynoecial primordia as they are carried up with the extending ovary wall. Concurrently, growth between and at the base of the gynoecial primordia initiates the three septa, which eventually become appressed

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at only their upper inner margins. Two placentae form initially as slight protrusions along the base and on each side of a septum. In each of the three locules or chambers of the ovary, there are two placentae—one from each septum (fig. 1). The ovules will develop from these placental bulges in the second growing season (Sattler 1973). Botanically speaking, an ovule is a megasporangium; i.e., a structure that bears the megaspore mother cell (MMC) (Davis 1966).

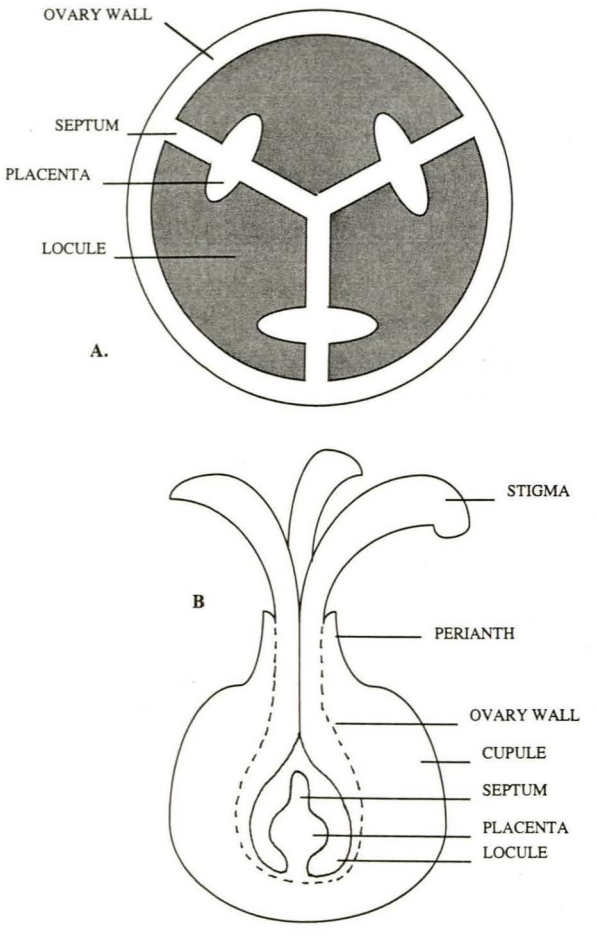

Figure 1.—*A Q. rubra pistillate flower at the time of pollination. 1A. Cross section of an ovary, showing three septa that divide the ovary into three locules or chambers. A locule contains two placentae or primordial bulges, each of which will differentiate into an ovule. Only one of the six ovules will mature into an acorn. 1B. Longitudinal section of a flower at the time of pollination, with two of the three locules shown.*

Between late July of the first season and early April of the second, only the cupule (the future acorn cup) develops further, enclosing the flower during the winter, with only lignified vestiges of the styles and perianth above its rim. By early May of the second season, the ovary wall has expanded, the placental axis has elongated, and the ovules bear the rudiments of the inner and outer integuments (Langdon 1939). By mid-May the nucellus is now covered by the inner and outer integuments, which have elongated over the end of the nucellus and have formed a "hole" called the micropyle. At the time of fertilization the margins of the outer integument, toward the open end, greatly increase in height and form a lip (Sattler 1973). This is the route through which the pollen tube approaches the embryo sac (Benson 1894). Major food reserves of starch and lipid are located almost exclusively within the outer integument, while the inner integument is virtually void of food reserves (Mogensen 1973). The MMC undergoes meiosis or reduction-division, producing four haploid cells, only one of which survives to become the functional megaspore. By a series of mitotic divisions, the megaspore gives rise to the megagametophyte or embryo sac, an eight-nucleate structure at the tip of the nucellus (fig. 2). A feature of the *Q. rubra* nucellus during growth of the megagametophyte is the appearance of a central strand of procambial elements that extend through the base of the nucellus and are continuous with the vascular tissues of the raphe and funiculus (Langdon 1939).

Once the embryo sac is formed, fertilization of its egg and central cell via germinating pollen must occur for seed development to continue. During fertilization, the pollen tube discharges two haploid gametes into the embryo sac. One fuses with the egg to produce a diploid zygote; the other gamete fuses with the 2N central cell (formed by the earlier fusion of the two polar nuclei) to produce the 3N (triploid) endosperm. Following fertilization, a free-nuclear endosperm grows before the first division of the zygote occurs (Hjelmqvist 1953, 1957; Brown and Mogensen 1972). In general, as the endosperm becomes cellular, the embryo begins to differentiate (Singh and Mogensen 1976), moving quickly through the heart-shaped stage (fig. 3).

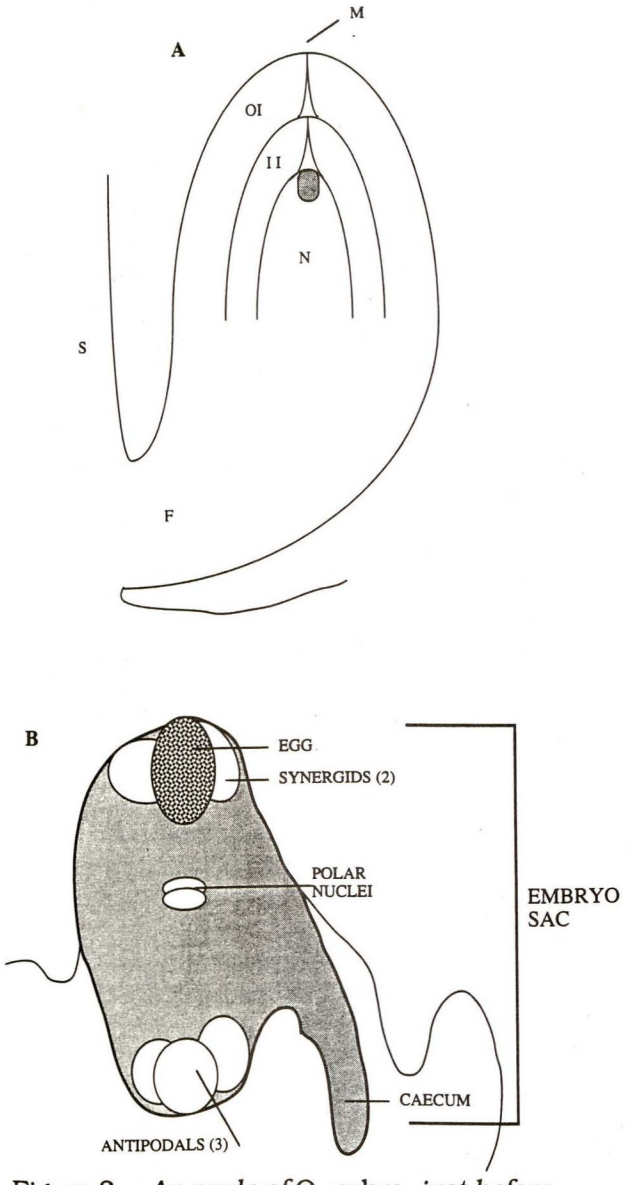

Figure 2.—*An ovule of* Q. rubra, *just before fertilization. 2A. The nucellus (N) is surrounded by the inner integument (II) and the outer integument (OI). The funiculus (F) attaches the ovule to the septum (S). 2B. The embryo sac contains the egg nucleus and seven other nuclei. Upon fertilization, the egg and pollen gamete fuse to become a zygote; and the two polar nuclei, which previously had fused to become the central cell, fuse with the other pollen gamete to become the triploid endosperm.*

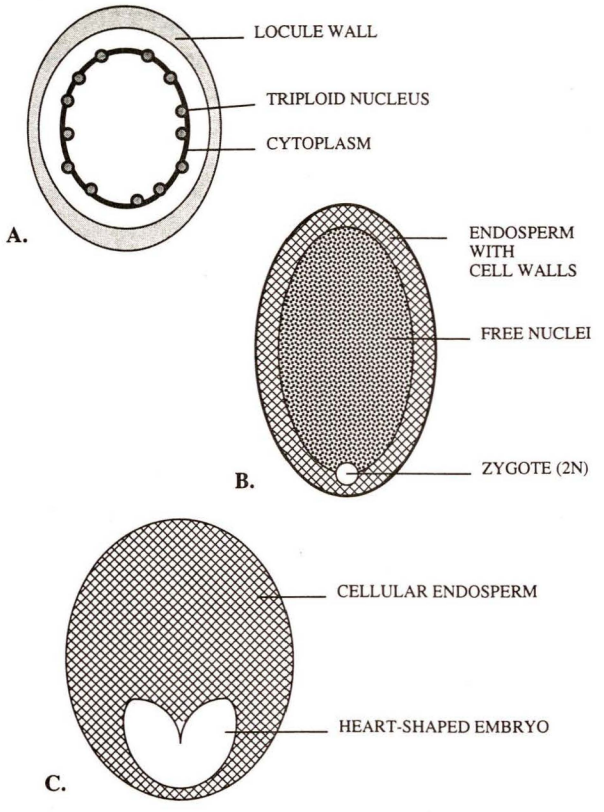

Figure 3.—*Some embryological stages of* Q. rubra. *3A. The free nuclear endosperm. Nuclei are triploid (3N) and exist in a common cytoplasm; i.e., there are no cell walls separating the nuclei. 3B. As the endosperm begins to form cell walls centripedally between the free nuclei, the diploid zygote begins to grow into a proembryo. 3C. The embryo is at the heart-shape stage when the endosperm becomes completely cellular. The "wings" of the embryo are the cotyledons that will grow and eventually fill most of the acorn.*

Information about later embryo and cotyledon growth of acorns is very limited. Mogensen (1965) provided the most detailed picture in his comparative study of *Q. alba* and *Q. velutina*. One major difference he noted between the two species was that the epicotyl apex of *Q. alba* produced from three to five leaf primordia before acorn maturity, but *Q. velutina* produced none. Stairs (1964) also found no leaf primordia in mature embryos of *Q. coccinea*.

STAMINATE FLOWERS

When we mention flowers, we tend to think only of the pistillate flower that gives rise to the

acorn. But there is another flower on the tree: the staminate or male flower that is the source of pollen.

The origin of the staminate flowers is similar to that of the pistillate flowers, except that the inflorescence or catkin on which they are assembled differentiates from a meristem in the axil of a bud scale, not a leaf. The first sign of differentiation of the staminate inflorescence primordium in those white oak species studied appeared from late May to July. The inflorescence is without appendages until late June or early July, when meristematic areas appear on the axis (Merkle *et al.* 1980). These floral apex primordia appear before or coincident with the subtending bract primordia (Turkel *et al.* 1955). However, Sattler (1973) found that the ovate-shaped floral apex of the staminate flower in *Q. rubra* was initiated in the axil of a small ridge-shaped bract close to the apex of the inflorescence, just the opposite of where the female apex forms on its inflorescence. The perianth members arise on the flanks of the floral apex in a spiral sequence; however, the sequence of stamen initiation is quite regular. The stamen primordia appear on the apex opposite the perianth members from mid-July to late July. By fall, these stamen primordia grow into immature anthers and filaments. The overwintering condition of the slightly lobed anther is that of a homogeneous parenchymatous mass.

Anther development resumes in early March to late April, varying by species and location. In higher plants, the parenchymatous mass differentiates into the sporogenous mass, its cell numbers increase mitotically, and eventually they undergo meiosis to become microspores and, finally, pollen grains. For oaks, there is only a pictorial account of meiotic stages *per se* as provided by Stairs (1964). Thus, there is a need for research on the entire topic of oak pollen development.

Dehiscence of pollen grains occurs about 6 weeks after differentiation of the anther tissues begins (Turkel *et al.* 1955). Before leaf flush, the staminate inflorescence of *Q. rubra*, bearing numerous staminate flowers, elongates and emerges from the bud scales as the familiar catkin (Vogt 1969). At first the catkins are erect and clustered, but they soon elongate further and droop (fig. 4). During maturation of the

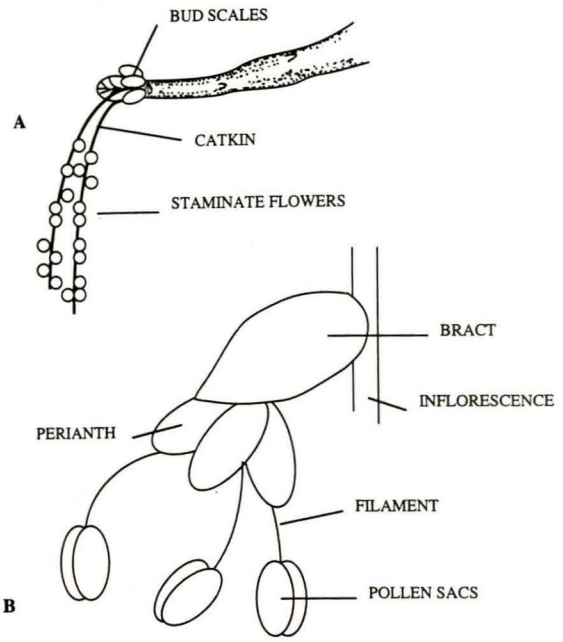

Figure 4.—*Catkins (inflorescences) (A) emerge from the axils of bud scales. Staminate flowers (B), bearing the pollen grains, are assembled along the length of the catkin.*

male flowers, the female flowers continue to develop in the axils of expanding leaves of the new shoot.

One to two weeks after the catkins appear, the small anther sacs split open to expose the pollen grains (fig. 5). Pollen shedding is usually complete in 3 to 4 days. The time of pollen shed is probably the best local index of the beginning of the visible portion of the seed production cycle. If relative humidity is high at time of pollen maturity, the pollen sacs may not split open. Wolgast (1972), using growth chambers, demonstrated that relative humidity at the time of pollen shed and stigma receptivity can limit the size of an acorn crop. No pistillate flowers survived when relative humidity exceeded 61 percent because the anther sacs did not open; but about half the flowers matured into acorns when relative humidity was lower. Continued cool, rainy weather may cause overripe male flowers to fall from the trees without shedding, resulting in a poor seed crop. Variation in date of flowering within a crown and among trees within a stand may offset some of the pollen loss related to weather conditions.

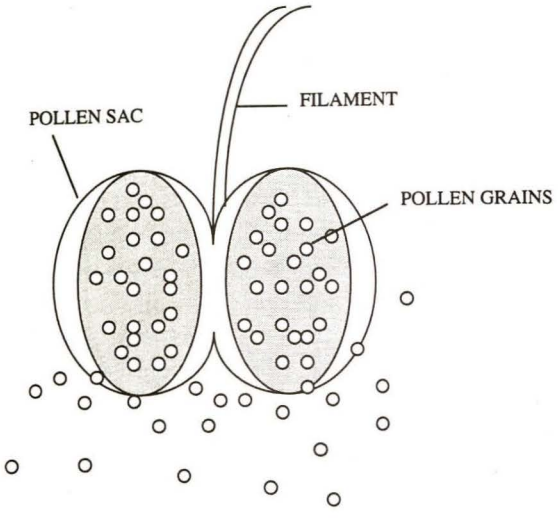

Figure 5.—*Pollen grains are released from the pollen sacs when suitable temperature and relative humidity conditions have been met.*

There have been conflicting observations about the dynamics of pollen tube growth after the pollen grain lands on the stigmatic surface. For instance, Benson (1894) did not find pollen tubes in *Q. robur*, a white oak, until just before fertilization. Jovanovic and Tukovic (1975) observed that pollen germination in *Q. robur* was completed within 24 hours, but fertilization occurred 6 to 7 weeks later, suggesting that pollen tube growth did not proceed until the ovule had completed development. In contrast, Allard (1932) observed that "When pollen reaches the stigma of members of the white oak group, the growth of the pollen tube containing the male cells follows an uninterrupted advance into the tissues of the style until the ovules are fertilized." These conflicting observations of pollen tube behavior for members of the same subgenus and species suggested that an investigation of this anomaly was required. Cecich (unpublished data) observed pollen tube growth in *Q. rubra*, *velutina*, and *alba* with fluorescence microscopy. All three species had the same pattern of pollen tube growth soon after the pollen grains landed on the stigmas of the pistillate flowers. Within 24 hours, the pollen tube germinates from the pollen grain and penetrates the epidermis of the stigma. A callose plug is synthesized to seal off the contents of the tube from the pollen grain; and the pollen grain falls off the stigma. The pollen tubes grow through the transmitting tissue of the stigma for about 3 weeks, where they cease growth just above the juncture of the three stigmas (fig. 6). The white oak pollen tubes resume growth toward the ovules in early June and enter the locules. Fertilization is accomplished by about June 15. In the two red oak species, *Q. rubra* and *Q. velutina*, the pollen tubes ceased growth, as noted, until the following growing season when pollen tube growth resumed and fertilization occurred in late May (*Q. rubra*) and late June (*Q. velutina*). Allard (1932) also found that in the red oak group the pollen tubes ceased growth at the base of the style until the following spring when the ovules were fertilized.

FACTORS AFFECTING REPRODUCTIVE SUCCESS

Acorn crops are the product of a long, arduous journey from the initiation of the flower primordium to the mature acorn. The differentiation of

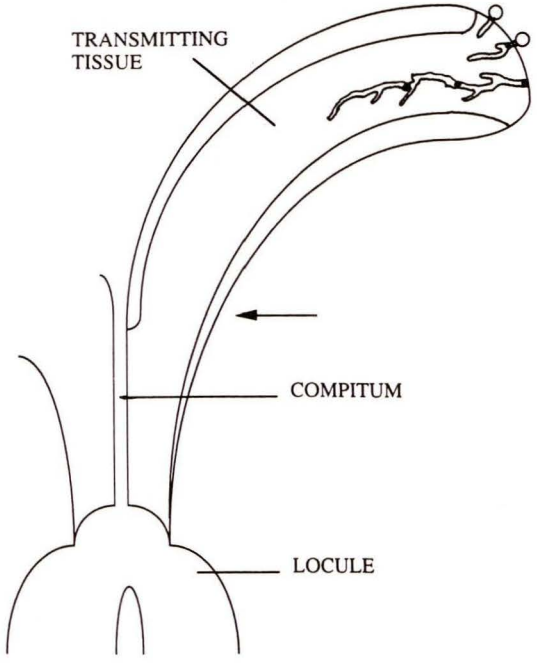

Figure 6.—*The stigma of a flower receives the pollen grains during pollination. After the pollen grains germinate, the pollen tubes grow partially through the transmitting tissue of the stigmas and cease growth after several weeks (arrow). In the second growing season, pollen growth resumes and the tubes enter the compitum, a free space between the three styles, where they proceed into the locule to fertilize the egg.*

reproductive structures extends from the primordium stage in late May (year one), through pollen shed and female receptivity (year two), and finally fertilization, embryogenesis, and maturation (year three). Over that length of time, what causes an acorn crop to succeed or fail?

Except for deep freezes in late spring (Sharp 1958, Sharp and Sprague 1967, Goodrum *et al.* 1971, Wolgast and Trout 1979), does the weather affect differentiation? Probably the most important factor controlling the emergence of pistillate flowers in the spring and their receptivity is temperature, which directly or indirectly influences flower emergence through branch and leaf elongation. Emergence of the staminate inflorescence and shedding of pollen are known to increase or hasten with rising temperatures and to slow with decreasing temperatures (Romashov 1957). Rainy weather, associated with decreased temperature, also decreased pollen dispersal. Mature pollen is more resistant to frost than anthers or the filaments of the catkins (Sharp 1958, Sharp and Sprague 1967). Pollen tube growth may also be affected by temperature, thus influencing the northern boundaries for the species range (Jicinska and Koncalava 1978). Sork *et al.* (1993) studied flower and acorn production in the same population of northern red, black, and white oaks for 8 years. They suggested that these three species have inherent cycles of reproduction that are modified by weather conditions—black oak with a 2 year cycle, white oak with 3 year cycles, and northern red oak with 4 year cycles. However, they concluded that the patterns of acorn production were not simply responses to weather events, but were also a function of prior reproductive history.

Genetic control over seed production in oaks has been demonstrated by a number of investigators. During 6 years of observation, Grisez (1975) found no *Q. rubra* seed crops that were better than poor. He did not observe flower crops because pistillate flowers were difficult to see from the ground. Grisez stated that his observations confirmed other reports that seed-producing capacity is, to a large extent, genetically controlled by the female parent. Farmer (1981) found that in a given year seed production among clones of northern red oak was most highly correlated with the percentage of pistillate flowers that were fertilized; while year-to-year differences were associated with variation in the number of flowers. He believed that fecundity could be increased by selecting high-yielding clones in a grafted orchard. Grafting of oak scions selected from mature, flowering individuals can be readily accomplished and, thus, flowers can be made quickly available (Irgens-Moller 1955). Ledig *et al.* (1971) and Wright (1953) also found much tree-to-tree variation in reproductive ability.

Schlarbaum and Rhea (unpublished data) evaluated flowering in a 17-year-old *Q. rubra* seedling seed orchard in Tennessee. They selected a light-, medium-, and heavy-flowering tree and counted all pistillate flowers. The majority of flowers were located in the upper one-third of the crown of each tree, and flower numbers did not differ among the four quadrants in a crown. Sharp and Chisman (1961) found that pollen catkins were evenly distributed across the crown of mature *Q. alba*. I have also observed the latter in *Q. alba*, *Q. rubra*, and *Q. velutina*.

Insects can have a big impact on acorn crops. Most accounts are about weevils (*Curculio* spp. and *Conotrachelus* spp.) as they destroy acorn crops (Gibson 1964, Kearby *et al.* 1986). However, weevils do not oviposit until midsummer, when the embryo's cotyledons are enlarging. But, most of the potential seed crop has been lost through flower abortion before then (Cecich 1993; Cecich *et al.* 1991), suggesting that weevils are not the major insect cause of poor acorn crops. Treehoppers (Membracidae) are another group of insects that deserve attention. These sucking insects can spend their entire life cycle in the crown of an oak tree (Kopp and Yonke 1973a,b,c, 1974). The late instars and young adults actively feed on any meristematic tissue, *including flowers*, during May and early June, just when most of the flower abortion happens (fig. 7). We observed these insects feeding on flowers that then died 1 week later (Cecich *et al.* 1991). Controlled feeding experiments are being done at this time to better elucidate the role of treehoppers in flower abortion.

Several authors have concluded that the size of an acorn crop is not related to the size of a flower crop; i.e., the appearance of numerous pistillate flowers in the spring does not guarantee numerous acorns (Sharp 1958, Sharp and

Chisman 1961, Wright 1953, Gysel 1956, Cecich *et al.* 1991, Sork and Bramble 1993). Factors that inhibit or enhance flower development, pollination, fertilization, and embryogenesis appear to be more important in determining the success of a seed crop.

As was noted earlier, little information is available about the reproductive biology of *Q. rubra*. In fact, no complete detailed life history for any species of oak has been written. Therefore, our knowledge of oak flowering biology is based on a few reports about selected events in only a few species. These references are often combined to tell a developmental "story" about a hypothetical oak—an oak that probably does not exist. Before we try to interpret how various factors influence the production of flowers and acorns, we must develop a solid understanding of the reproductive cycle of individual species. The fragmented information about oak flowering does not give us an accurate picture of the flowering process, but it does indicate where the shortcomings and opportunities exist. We can then ask meaningful questions and do the appropriate research. We must study the biology of *Q. rubra* if we are truly interested in managing *Q. rubra* acorn crops.

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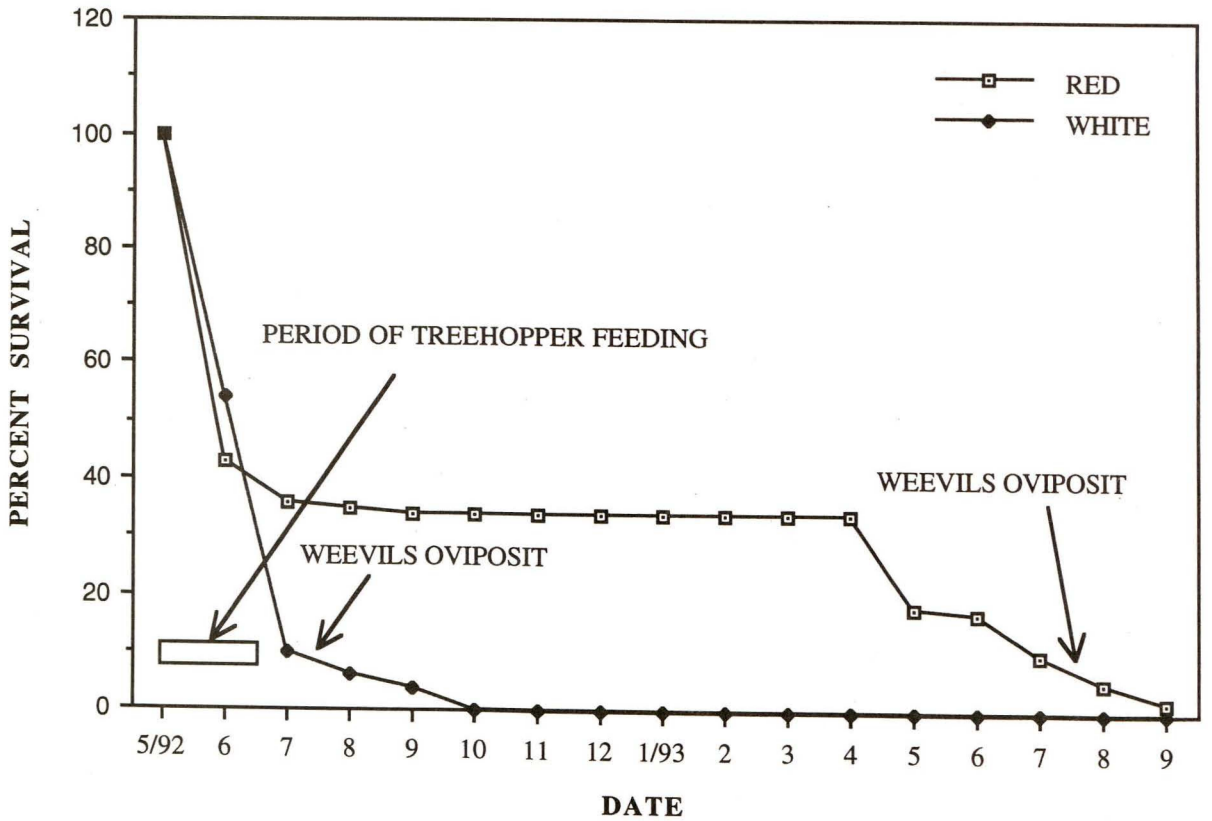

Figure 7.—*A typical survival curve of the oak pistillate flowers. White oak takes one growing season to produce its acorn crop; red oak requires two. Most of the flower loss occurs in May and early June, when treehoppers are actively feeding. Inadequate pollination may also contribute to the early abortion. Weevils oviposit after most of the potential seed crop has aborted. In either species of oak, less than 5 percent of the flowers usually survive to become acorns.*

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Carbon Fixation and Allocation in Northern Red Oak

J.G. Isebrands, P.T. Tomlinson, and R.E. Dickson

In North America, northern red oak (*Quercus rubra* L.) ranges from Minnesota northeast to Nova Scotia and south to Georgia and Louisiana (Harlow and Harrar 1958, Burns and Honkala 1990). Moreover, northern red oak hybridizes readily with other co-occurring red oak species, making its adaptability and genetic influence even more widespread across eastern forests (Jensen *et al.* 1993). It is highly valued for lumber and veneer, and is an important tree for wildlife food, biodiversity, and aesthetics. But, northern red oak is difficult to regenerate either naturally or artificially even after many years of silvicultural research (Crow and Isebrands 1986, Crow 1988, Johnson 1994). In fact, northern red oak seedlings typically exhibit slow early growth and experience dieback in most field environments. Also, nursery stock is often characterized by variable growth and poor quality.

If the processes regulating oak seedling growth were more clearly understood, this knowledge could be used to develop physiologically based strategies for managing the species. Unfortunately, there is a lack of fundamental knowledge of the physiological processes controlling early growth and development of northern red oak compared to many trees. Until recently there have been few studies on carbon fixation and allocation in northern red oak (Kramer and Decker 1944, Farmer 1975, Chabot and Lewis 1976, Hinckley *et al.* 1978, Heichel and Turner 1983, Jurik 1986, Dickson *et al.* 1990, Tomlinson and Dickson 1992). This lack of fundamental information on carbon budgets is of concern because carbon allocation within plants is a major determinant of growth (Dickson 1989, 1991). Knowledge of how carbon fixation and allocation change in response to changing environmental conditions could help us better understand a plant's performance in natural environments. Moreover, carbon fixation and allocation are tightly linked with acquisition of other resources, such as nitrogen and water (Pearcy *et al.* 1987). Understanding carbon budgets in northern red oak could also help us identify attributes that could be manipulated through different management practices (Dickson *et al.* 1990). For example, such understanding may lead to improved management practices for natural regeneration or nursery production; in addition, it could provide information on the potential impact of environmental stress on growth (Dickson and Isebrands 1991). However, basic information on carbon budgets of northern red oak should be developed first under standard environmental conditions. Then, patterns of carbon fixation and allocation can be determined and interpreted under stress conditions, such as drought or anthropogenic pollutants (i.e., SO_2, O_3, and acid deposition) (Dickson and Isebrands 1991). In this paper we review what is known about carbon fixation and allocation in northern red oak. Emphasis will be on seedlings grown in a controlled environment with some reference to companion field studies. We will show that patterns of leaf development, carbon fixation, and carbon allocation in northern red oak are not typical of the patterns commonly found in most temperate tree species with similar simple-leaf forms.

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LEAF DEVELOPMENT

Growth of northern red oak occurs in episodic flushes with cycles of shoot growth and apparent rest (Borchert 1975, Reich *et al.* 1980, Isebrands *et al.* 1988, Dickson 1994). Shoot growth progresses from a bud stage, to a linear stem growth stage, to a linear leaf growth stage, to a lag stage (apparent rest); then the cycle is repeated (Hanson *et al.* 1986). Within-leaf development in northern red oak is acropetal and physiological leaf maturation continues past full leaf expansion, unlike that in most temperate tree species with simple leaves (Tomlinson *et al.* 1989, 1991). In controlled

environments, several episodic flushes may occur, depending upon environmental conditions and culture. In nurseries, northern red oak seedlings usually exhibit two or three flushes in a season in the northern part of the species' range and four to five in the southern part (P. Kormanik, personal communication). In the field, seedlings have one to two flushes in the north and two to three in the south, depending upon environmental conditions. The number of leaves within a flush varies with age and size of seedling. The first flush has 3 to 7 leaves, the second 5 to 10, and the third 8 to 15 (Hanson *et al.* 1986). Freely growing coppice shoots can have many leaves and may even approach an indeterminate shoot growth pattern (Cobb *et al.* 1985). Moreover, the number of leaves in a flush and the timing of flushing are under genetic control (Farmer 1975).

Knowledge of the seedling developmental stages and leaf maturation patterns is essential for studies of carbon fixation and allocation in northern red oak. Without careful attention to the exact stage of development, investigators can easily confound and misinterpret carbon fixation and allocation patterns (Dickson 1989, 1991). We developed a *Quercus* morphological index (QMI) to avoid these problems (Hanson *et al.* 1986, Dickson 1994). The QMI is based on simple leaf and stem growth measurements of northern red oak seedlings. Four distinct stages have been defined for each flushing episode—bud swell (Bd), linear stem elongation (SL), linear leaf elongation (LL), and lag (Lg) (fig. 1). The QMI is used for carbon fixation and allocation studies of northern red oak in several ways (Isebrands *et al.* 1988): (1) to ensure uniformity of morphological stages of development in parallel studies of the same seed source at different locations, (2) to compare seed sources from year to year, (3) to determine shifts in plant development due to different treatments or environments, and (4) to relate the morphological stages of seedling development to specific biochemical, physiological, and anatomical events and processes. The QMI is used throughout the remainder of this paper.

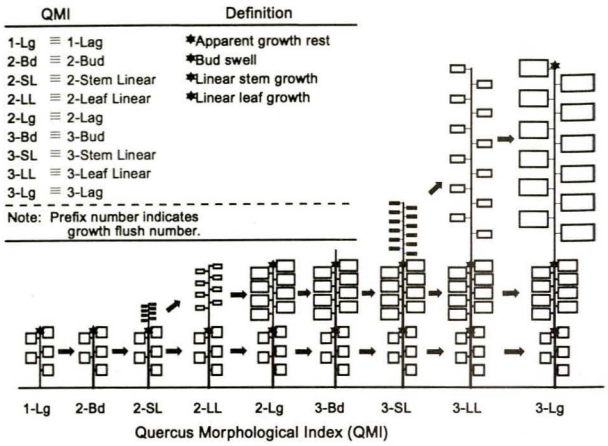

Figure 1.—*Definitions of* Quercus *morphological index (QMI) stages and schematic of the development of a typical three-flush northern red oak seedling according to QMI (from Hanson* et al. *1986).*

CARBON FIXATION

Carbon fixation in northern red oak trees varies widely with stage of leaf development, tree age, and environmental conditions. We refer to carbon exchange rate (CER; umol CO_2 $m^{-2}s^{-1}$), or net photosynthetic rate, as our definition of carbon fixation. In northern red oak seedlings growing under optimal conditions in controlled environments, light-saturated CER increases during leaf development (Hanson *et al.* 1988a) (fig. 2) and continues beyond full leaf expansion before declining (Hanson *et al.* 1988a, Tomlinson *et al.* 1991) (fig. 3). In first-flush leaves, CER increases from the 1-SL stage to the 2-LL stage, decreases during 2-Lg, then increases again during the third flush. The CER of second-flush leaves follows this same pattern, increasing from 2-SL to 3-SL before decreasing during 3-Lg (fig. 2). The maximum CER recorded under controlled environment conditions (i.e., 400 umol photosynthetic photon flux density) is between 7 and 8 umol $m^{-2}s^{-1}$ (Hanson *et al.* 1988b).

First-flush leaves of northern red oak seedlings do not attain maximum CER until the plant reaches the leaf linear stage of the second flush (2-LL), well after the first-flush leaves have stopped expanding (figs. 2 and 3). This pattern distinguishes northern red oak (and perhaps other oaks) from most temperate trees with simple leaves in which CER usually peaks at or near full leaf expansion (fig. 3). The continued increase in CER beyond full leaf expansion in oak is a result of the continuing development of photosynthetic pigment and enzyme systems rather than leaf anatomical differentiation (Isebrands *et al.* 1988, Tomlinson *et al.* 1991).

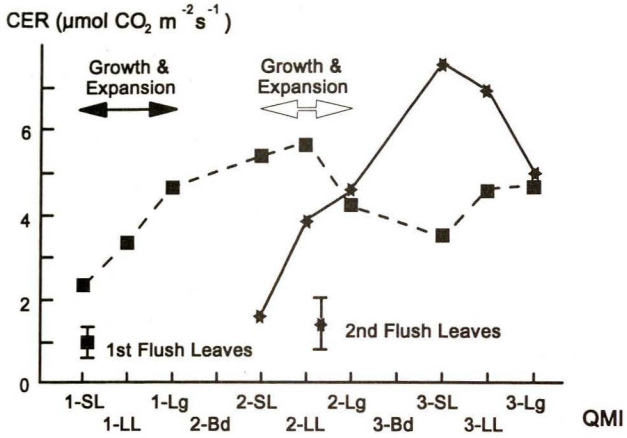

Figure 2.—*Light-saturated carbon exchange rate (CER) of first- and second-flush leaves during development of a three-flush northern red oak seedling grown in a controlled environment. Data are plotted as a function of QMI stage. Error bars are the 95 percent confidence intervals for first- and second-flush leaves as indicated.*

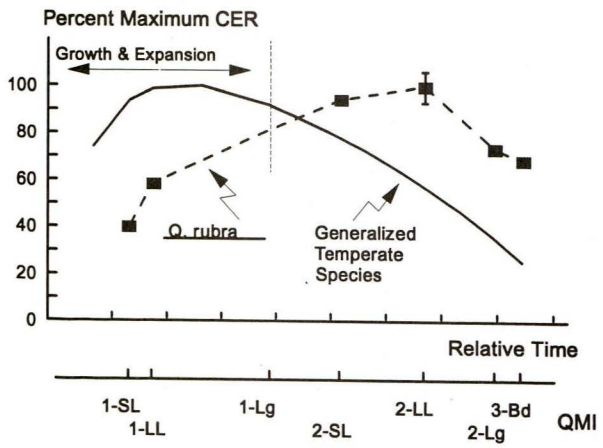

Figure 3.—*Percent of maximum light-saturated carbon exchange rate (CER) as a function of QMI (dashed line) or relative time (solid line). Error bar given for northern red oak data is the 95 percent confidence interval. Solid line depicts a typical curve for CER of most temperate tree species. The period of leaf growth and expansion for both curves is depicted by the horizontal arrow.*

Dark respiration in northern red oak seedlings grown in controlled environments is highest (most negative) during leaf expansion (i.e., SL and LL) and decreases to the lowest (least negative) rate at 100 percent leaf expansion (i.e., Lg). It is stable thereafter through subsequent flushes, averaging -0.5 to -1.5 umol $m^{-2}s^{-1}$ (Hanson *et al.* 1987b, 1988a). Other investigators have confirmed these respiration rates in the field (Heichel and Turner 1983, Jurik 1986).

Carbon fixation rates in northern red oak leaves in the field are more variable than in controlled environments; however, the number of reports on this subject is limited. In a drought experiment in which field-grown saplings were transplanted into the greenhouse, Hinckley *et al.* (1978) found that northern red oak exhibited rather low CER with an upper asymptote of 5.7 umol $m^{-2}s^{-1}$. CER peaked at 26° C, but dropped dramatically when temperatures approached 40° C. Drought significantly decreased CER to about 1.5 umol $m^{-2}s^{-1}$, but rates recovered soon after rewatering. In addition, Heichel and Turner (1983) studied CER of northern red oak saplings in the field before and after simulated insect defoliation. CER's were between 5 and 8 umol $m^{-2}s^{-1}$, depending on light conditions. Maximum CER occurred in July and August and then decreased in September and October. CER increased in leaves remaining after defoliation, partially compensating for the adverse effects of defoliation. In a study of CER in mature overstory northern red oaks, Jurik (1986) found that CER varied with light conditions, season, and year. CER of leaves in the top of the canopy reached 14 umol $m^{-2}s^{-1}$ during one season, while CER in the understory leaves was only 6.7 umol $m^{-2}s^{-1}$. We can conclude from these field studies that leaves of mature northern red oak maintain a rather high level of CER through much of the growing season unless they are subjected to stress such as drought or defoliation (Hanson *et al.* 1987a).

CARBON ALLOCATION

Terminology

In the scientific literature, there are differences of opinion and confusion about the terminology associated with carbon allocation studies. The terms carbon allocation, carbon partitioning, and biomass components are often used interchangeably, but have very different meanings (Dickson and Isebrands 1993). We prefer the

following terminology and will use it throughout this paper. Carbon allocation refers to carbon distribution within the plant. Carbon partitioning refers to carbon flow among different chemical fractions (e.g., transported chemicals, or storage pools). Allocation and partitioning are usually determined with ^{14}C labeling (Isebrands and Dickson 1991). Biomass components (i.e., leaves, stem, roots, etc.) are mensurational parameters that are usually presented as oven dry weights and are the result of the more mechanistic process parameters, carbon allocation and partitioning.

Distribution

Distribution of current photosynthate from first-flush leaves of northern red oak seedlings grown in controlled environments is directly related to plant developmental stage, or QMI (Dickson and Isebrands 1987, Isebrands and Dickson 1987, Dickson *et al.* 1990). ^{14}C fixation and translocation patterns (fig. 4) mirror CER patterns (fig. 2), while the quantity of ^{14}C retained in the source leaf is inversely related to that transported from the leaf (Dickson 1991, p. 65). ^{14}C transport

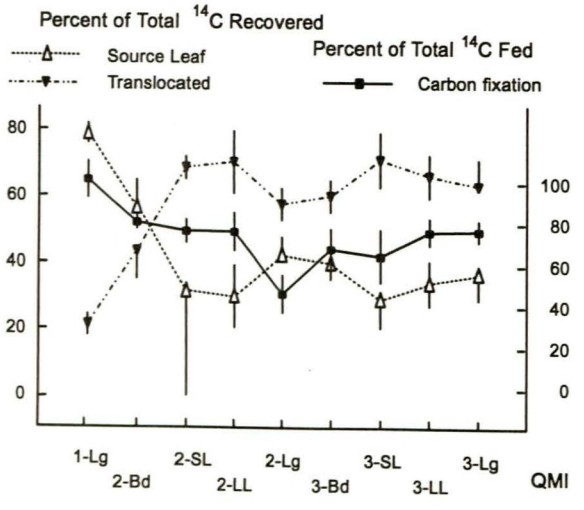

Figure 4.—*Changes in ^{14}C fixation by, ^{14}C retention in, and ^{14}C transport from first-flush leaves of northern red oak seedlings grown in a controlled environment as a function of developmental stage (QMI). ^{14}C fixation was determined immediately after a 30-minute photosynthetic exposure of the source leaf to $^{14}CO_2$ and is expressed as a percentage of the $^{14}CO_2$ supplied. ^{14}C retention in and transport from the source leaf were determined 48 hours later and are expressed as a percentage of the total ^{14}C recovered at harvest (48 hours).*

from a first-flush source leaf increases from about 20 percent at 1-Lg to more than 70 percent at 2-SL, decreases during 2-Lg, then increases during the third flush. About 90 percent of the translocated photosynthate is transported upward to the developing stem and leaves during the second flush and about 90 to 95 percent is transported downward to the lower stem and roots during Lg periods (fig. 5). First-flush leaves also contribute photosynthate to developing third-flush leaves and stem, allocating about 50 percent of the translocated ^{14}C upward. These patterns all indicate that source leaf metabolism is strongly controlled by sink demand in northern red oak seedlings.

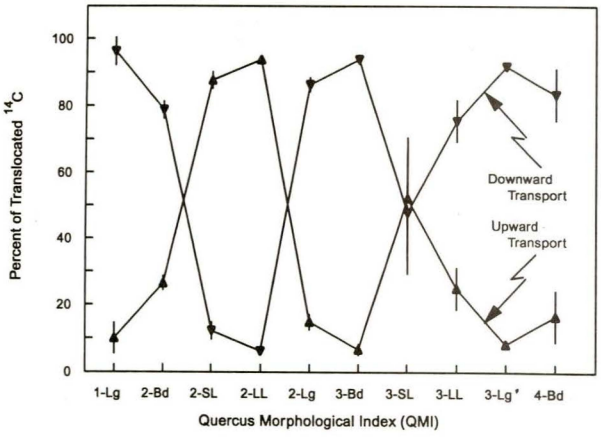

Figure 5.—*Upward and downward transport of ^{14}C-photosynthate from first-flush leaves as a function of QMI. Seedlings were grown in a controlled environment. Data are expressed as a percentage of the ^{14}C translocated out of the first-flush source leaf during 48 hours after photosynthetic exposure to $^{14}CO_2$.*

The transport pattern of ^{14}C from second-flush leaves is similar to that found for first-flush leaves, primarily upward during the third flush and downward during 3-Lg (Tomlinson and Dickson 1989). Of the photosynthate transported from a median second-flush leaf, about 60 percent is transported upward to developing leaves and stem during 3-LL, but only about 10 percent is transported upward during 3-Lg and 3-Bd stages (fig. 6). Moreover, during active shoot growth, basal second-flush leaves translocate more ^{14}C-photosynthate to the lower stem and roots than apical leaves, while apical leaves transport more to the developing shoot. However, these leaf positional differences are not

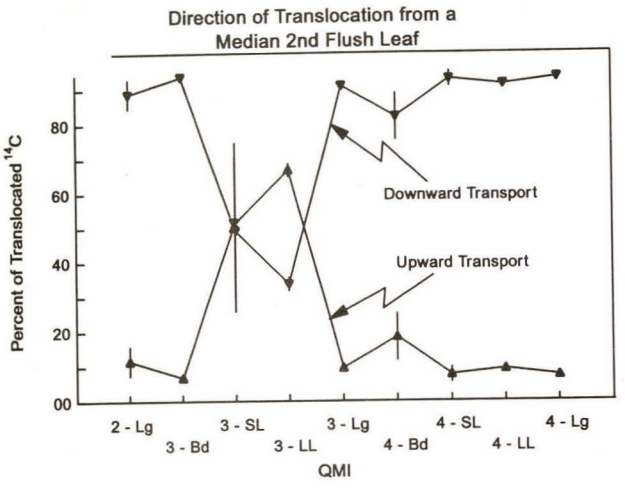

Figure 6.—*Distribution of ^{14}C-photosynthate from second-flush leaves as a function of QMI. Seedlings were grown in a controlled environment. Data are expressed as a percentage of the ^{14}C translocated out of the second-flush source leaf during 48 hours after photosynthetic exposure to $^{14}CO_2$.*

present in lag plants because essentially all transport is downward to the lower stem and roots. Thus, leaf position within a flush influences distribution only during active shoot growth (Tomlinson and Dickson 1989).

When ^{14}C transport patterns from first-flush leaves of northern red oak seedlings grown in controlled-environment growth chambers are compared to those from seedlings grown in the greenhouse and field, the patterns are similar if the plants were presented ^{14}C at the same developmental stage (figs. 7a,b,c). We have examined carbon allocation in potted plants (year 1) in the growth chamber and greenhouse as well as in a typical nursery bed (Tomlinson and Dickson 1992). When first-flush leaves are labeled with $^{14}CO_2$ at different developmental stages, the percent of ^{14}C exported during 48 hours from the first-flush leaves to developing second-flush shoots and roots are similar for all environments (fig. 7a). During development of the second flush, approximately 90 percent of ^{14}C exported from the first-flush leaves was transported to the developing shoot (fig. 7b). But, in the absence of active shoot growth, nearly all the ^{14}C exported was found in the roots (fig. 7c). Allocation within the plant is controlled by the changing sink strength of the developing leaves as defined by the developmental stage within the flush cycle. Differences in transport patterns in different environments are related to timing of each developmental stage (QMI) of the seedling. Time in days after emergence (DAE) required to reach a specific QMI stage is 5 to 10 days longer in field-grown seedlings than in seedlings grown in a controlled environment (fig. 8). Thus, carbon allocation patterns in northern red oak seedlings are related to plant developmental stages rather than some chronological time such as DAE.

Because of the above carbon allocation patterns, the variability seen in the developmental stages of northern red oak seedlings in nursery beds and in the field presents major practical management problems. Ideally, any silvicultural manipulation of northern red oak seedlings should take place at a uniform developmental stage. For example, undercutting of seedlings in the nursery should be done during the lag stage when photosynthate is being allocated to root systems and is available for new root growth. However, the variable rate of development among seedlings makes it difficult for managers to prescribe standard silvicultural practices designed to improve survival and early growth of northern red oak seedlings. That task would be less difficult if flushing variability could be decreased through genetic selection or improved nursery practices.

There has been little, if any, work on carbon allocation in mature northern red oak trees, although some possible guidelines are provided by McLaughlin *et al.* (1979, 1980), who studied seasonal changes of photosynthate and chemical fractions in leaves and branches of mature *Quercus alba* trees. They found that canopy growth and maintenance imposed a significant drain on photosynthate throughout the growing season. However, because there are physiological differences between species, similar studies in northern red oak are necessary.

Partitioning Among Chemical Fractions

Carbon partitioning among chemical fractions in leaves of northern red oak seedlings changes over time and with stage of plant development (figs. 9 and 10). When first-flush leaves at 1-Lg are fed $^{14}CO_2$, the percentage of ^{14}C in sugar decreases with time after treatment as sugar is metabolized or translocated from the leaf (fig. 9).

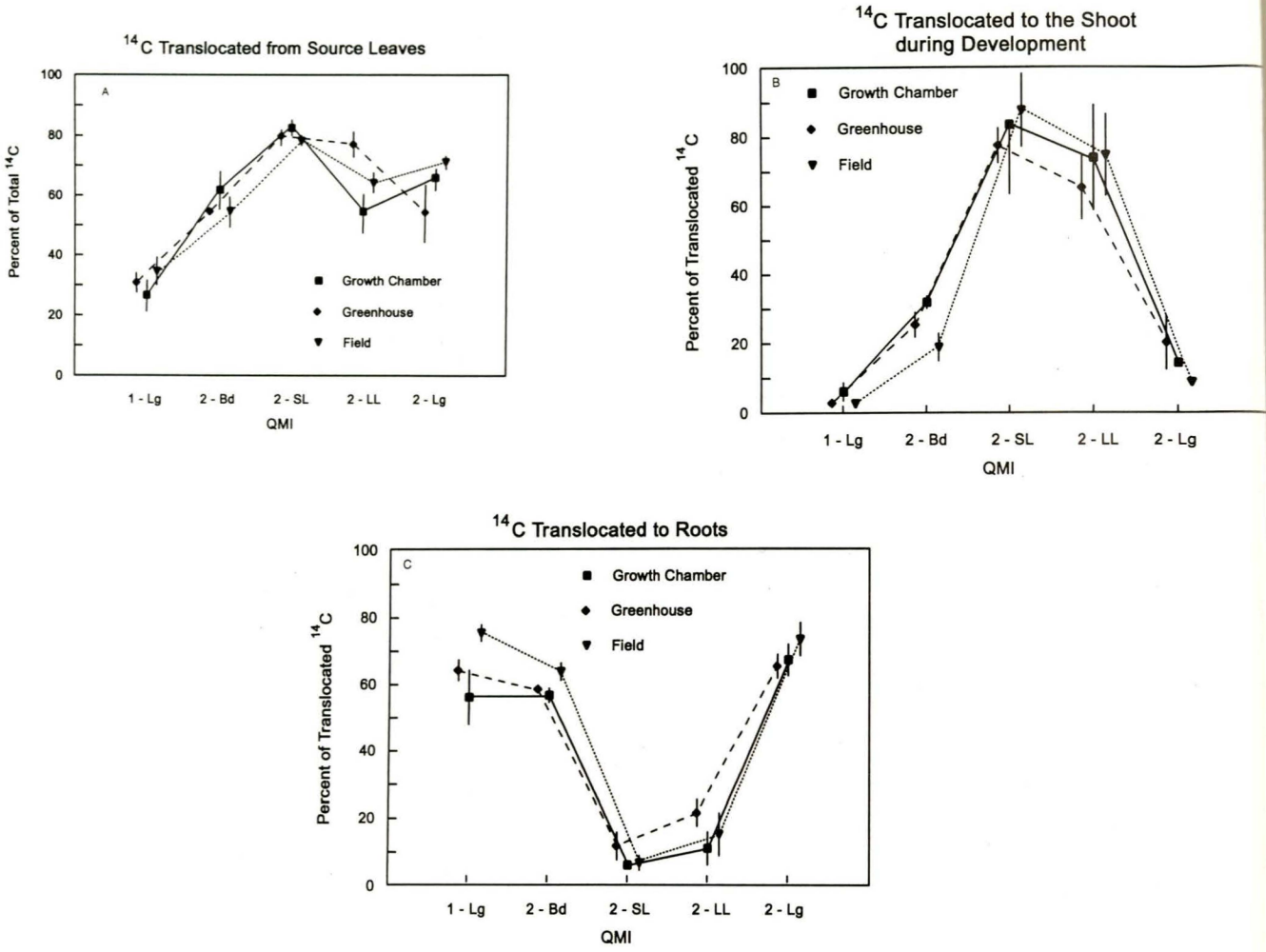

Figure 7.—*A comparison of containerized northern red oak seedlings grown in a controlled-environment growth chamber, greenhouse, and field: A. ^{14}C photosynthate distribution from first-flush source leaves. Distribution is expressed as the percentage of total ^{14}C translocated out of the source leaf into the second-flush shoot during 48 hours after photosynthetic exposure to $^{14}CO_2$, when the first flush was exposed to $^{14}CO_2$ at each QMI stage throughout development of the second flush; B. ^{14}C photosynthate translocated from the first flush to the shoot during the second flush; and C. ^{14}C photosynthate translocated to the roots from the first flush during the second flush.*

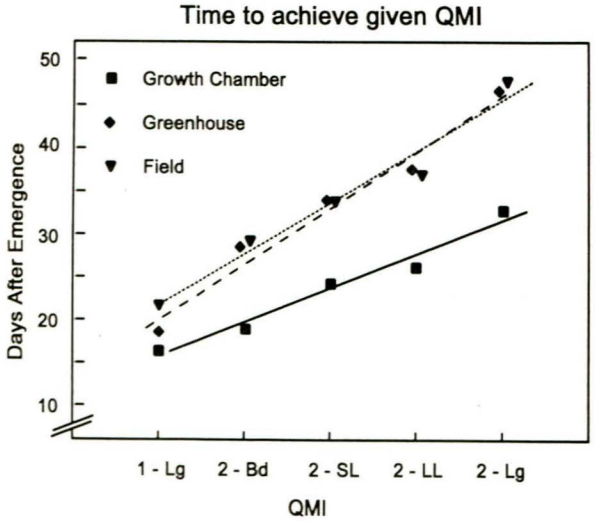

Figure 8.—*Rate of ontogenetic development in containerized northern red oak seedlings grown in a growth chamber, greenhouse, and field. Time required to achieve each QMI stage is plotted as a function of days after emergence (DAE).*

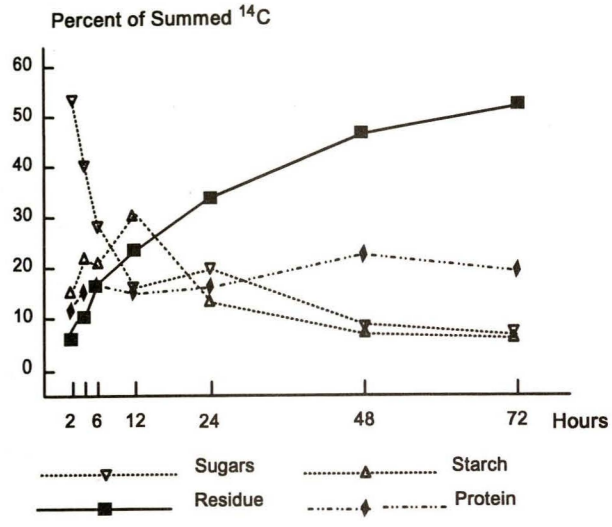

Figure 9.—*Partitioning of ^{14}C among chemical fractions in first-flush northern red oak leaves as a function of time (hr) after a 30-minute photosynthetic exposure of 1-Lg plants to $^{14}CO_2$. The residue fraction contains primarily structural carbohydrates. Components of the leaf were separated into four chemical fractions, using differential solubility, ion exchange, and enzymatic techniques; percentages given are based on the sum of ^{14}C recovered in the four chemical fractions (Isebrands and Dickson 1991).*

In contrast, the percentage of ^{14}C in the residue (i.e., structural carbohydrate) fraction increases with time, indicating continuing vascular development. The percentage of ^{14}C in starch increases during the light period (i.e., the first 12 hours), then decreases during the subsequent dark period. Starch storage in leaves during 1-Lg is primarily associated with the diurnal cycle of carbon storage. The starch accumulated during the light period is degraded in the dark to maintain sugar transport out of the leaf. The percentage of ^{14}C found in protein increases during the first 6 hours after treatment, then remains constant.

Partitioning patterns in the stem and roots after ^{14}C labeling of mature leaves are similar to those found in leaves (Dickson *et al.* 1990). In both stem and root tissue, the percentage of ^{14}C in sugars decreases and that in structural carbohydrates (residue) increases with time (fig. 10). In stems, ^{14}C in starch increases for 12 hours in the light, decreases during the dark period, then increases for the remaining period. This pattern indicates that stems have both diurnal and long-term starch storage pools. In roots, the percentage of ^{14}C in starch increases for 12 to 24 hours, then remains constant, indicating long-term storage. Taproots contain about three times as much ^{14}C starch as lateral roots do (data not shown). The ^{14}C content in protein of stem and root tissues increases during the first 12 hours, then remains constant for the rest of the chase period. Lateral roots contain almost twice as much ^{14}C protein as the taproot does (data not shown).

Like carbon fixation, carbon partitioning patterns in northern red oak are episodic and related to leaf growth and subsequent plant development (Dickson 1986, 1991; Dickson and Tomlinson 1988). The partitioning of recently fixed ^{14}C among different chemical fractions in first-flush source leaves changes dramatically when leaves are exposed to $^{14}CO_2$ and analyzed at different QMI stages (fig. 11). These changes reflect both maturation processes within the leaf and metabolic changes in carbon flow due to changing sink demands in the seedling. For example, almost 50 percent of the ^{14}C recovered in first flush source leaves at 1-Lg is found in residue. Although ^{14}C partitioning into residue decreases during each subsequent QMI stage through 2-Lg, more than 15 percent ^{14}C is still incorporated into residue at 2-Lg and later QMI stages, indicating continued vascular development well after full leaf expansion. The percentage of ^{14}C incorporated into protein increases from 1-Lg to 2-Bd, decreases to 2-Lg, then increases again at the beginning of the third flush. This pattern of protein synthesis indicates that physiological development continues well after full leaf expansion and shows a response (similar to that observed for CER) to increased sink demand during flushing episodes, perhaps indicating cyclic synthesis of Rubisco.

The percentage of ^{14}C recovered in both sugar and starch also changes with QMI. The ^{14}C remaining in the sugar fraction after 48 hours increases almost linearly from 1-Lg to 3-Lg, although there may be a slight cycle from 1- to 2-Lg and from 2- to 3-Lg. This sugar is probably a storage pool that increases with leaf age and does not respond to sink demand as do CER and translocation (figs. 2 and 4). ^{14}C incorporation into starch in first-flush source leaves at 1-Lg is primarily into the diurnal

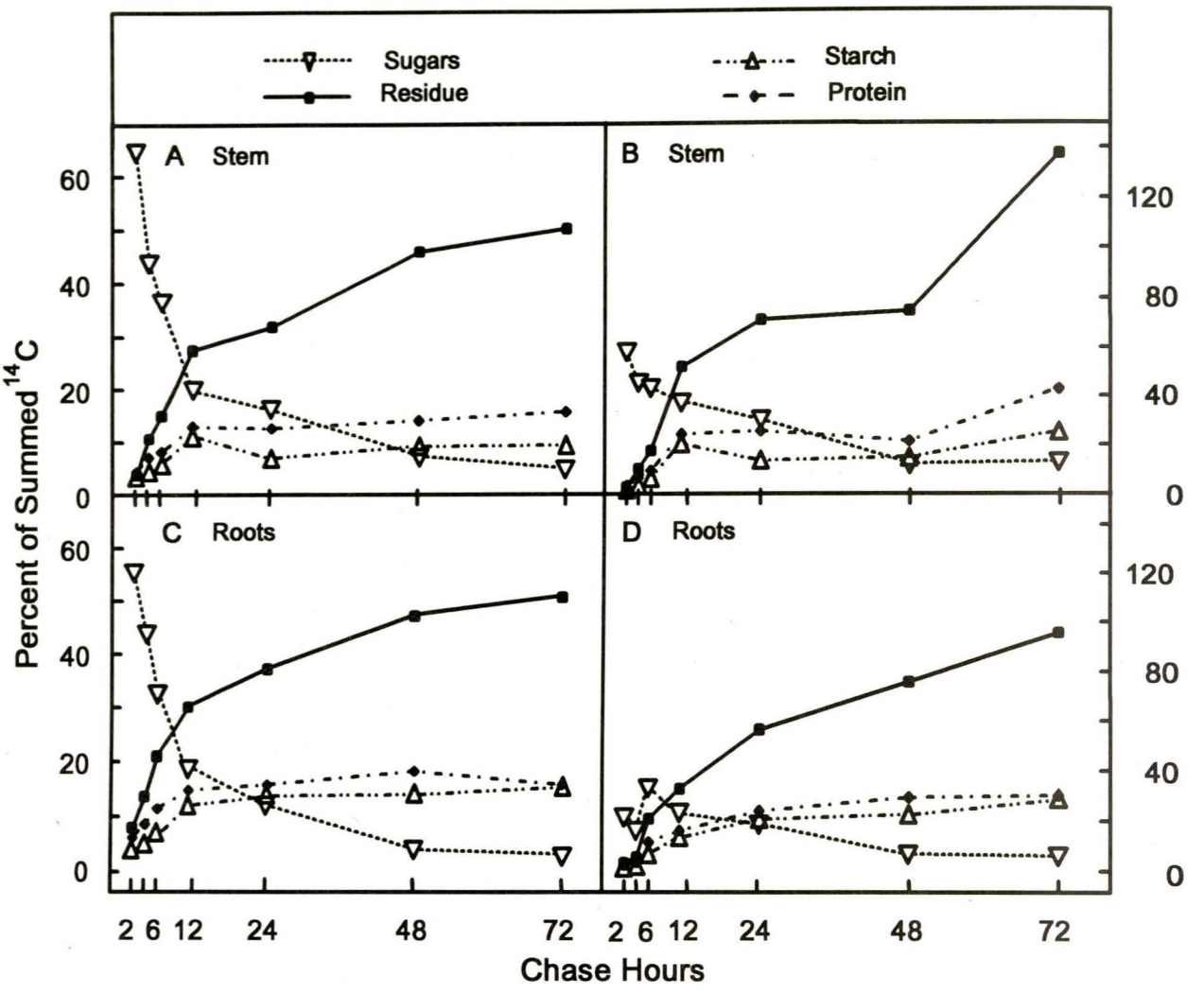

Figure 10.—*Changes in partitioning of ^{14}C among chemical fractions from stem and root sink tissues over time. A. and C. The ^{14}C present in each of four chemical fractions expressed as a percent of the summed ^{14}C from stem and root tissue, respectively. B. and D. The same data expressed as root tissue, respectively.*

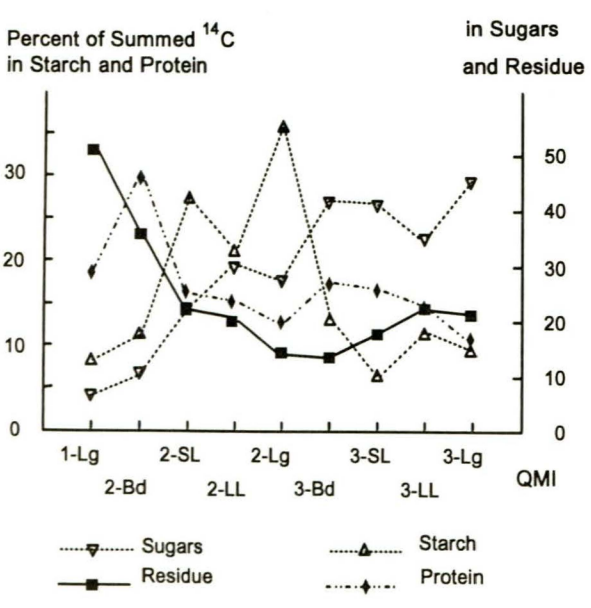

Figure 11.—*Partitioning of ^{14}C among chemical fractions in first-flush northern red oak source leaves as a function of QMI stage. Leaves were exposed to $^{14}CO_2$ for 30 minutes and harvested after 48 hours. The chemical fractions were then analyzed as described in figure 9.*

storage pool because less than 10 percent of ^{14}C is present in starch after 48 hours (figs. 9 and 10). In contrast, the percentage of ^{14}C found in starch increases from 1-Lg to 2-Lg, then decreases to 3-SL, then increases again. This partitioning pattern indicates that, in addition to diurnal storage, there is a long-term starch storage pool in northern red oak leaves that changes in size over development. ^{14}C incorporated into this starch storage pool may also reflect both the increasing physiological maturity of the source leaf (1-Lg to 2-Lg) and changing sink demand for assimilate (after 2-Lg).

The incorporation of ^{14}C into residue, starch, and sugars of both stem and taproot is also cyclic and varies with QMI. Although more total ^{14}C is recovered in each of these fractions during 2-Lg and 3-Bd when most transport is downward from source leaves (fig. 5), the percentage of ^{14}C decreases in residue and increases in sugar and starch (data not shown). This result indicates that both stem and taproot accumulate reserves during the lag period when more assimilate is available than needed for growth.

Carbon Budget

There have been few studies of carbon budgets in northern red oak. The paucity of studies is likely due to the lack of fundamental information on carbon fixation and allocation in the species in general and the difficulty in obtaining some of the measurements, such as root respiration, necessary for calculating carbon budgets. In one study on changing carbon budgets in response to simulated insect defoliation of 9- to 11-year-old northern red oak saplings, Heichel and Turner (1983) found defoliation significantly decreased carbon fixed from 69 g CO_2d^{-1} in control trees to 24 g CO_2d^{-1} in 75 percent defoliated trees. Even after the defoliated trees had produced new leaves, carbon fixation increased only to 38 g CO_2d^{-1}, much less than in undefoliated trees. Sixty percent of the increase in daily carbon fixation was attributed to new foliage, and the remainder was attributed to an increase in carbon assimilation rate of the remaining old leaves.

In another study on northern red oak seedlings at selected stages of growth (QMI's), Hanson *et al.* (1987a) examined the influence of light on carbon budgets. They estimated daily carbon gain of a three-flush northern red oak seedling growing in open conditions to be 1.7 g CO_2d^{-1}. Maximum CO_2 fixation occurred in full sunlight (1900 umol $m^{-2}s^{-1}$), and fixation did not decrease appreciably until there was more than 50 percent shade (500 umol $m^{-2}s^{-1}$). In heavy shade (less than 200 umol $m^{-2}s^{-1}$), daily carbon gain was always negative. This budget analysis suggested that small northern red oak seedlings growing under a full forest canopy or under dense vegetation do not receive sufficient light for photosynthesis to offset respiratory losses. Thus, mortality is likely. The silvicultural implications of these results are significant—larger seedlings are desirable to decrease competition, and an adequate light environment for the seedlings must be maintained through overstory manipulation and understory control.

SUMMARY

Carbon fixation and allocation patterns in northern red oak are episodic and closely related to leaf and plant developmental stage. Unlike most temperate trees, northern red oak has an acropetal pattern of within-leaf differentiation, and physiological leaf maturation continues past full expansion. Leaves of previous flushes are important contributors to the growth of subsequent flushes. Juvenile northern red oak seedlings growing in the field are dependent upon an adequate light environment to maintain a positive carbon balance and improve survival and early growth. Carbon fixation and allocation in northern red oak in field environments are similar to those in a controlled environment. However, more research is needed, and that research should be scaled up from the seedling level to larger trees and from tree crowns to forest canopies. This effort should include studies of carbon allocation during flowering and acorn production. Such research will provide valuable information needed to help ensure that northern red oak maintains its place in future forests.

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The Silviculture of Northern Red Oak

Paul S. Johnson

The natural range of northern red oak (*Quercus rubra* L.) spans several climatic and ecological regions in the Eastern United States and Eastern Canada (Sander 1990) (fig. 1). For that reason, it is difficult to generalize the species' silviculture because tree growth, competition, and factors affecting regeneration vary greatly among regions. Recent increases in the value of northern red oak for timber and wildlife, combined with threats from gypsy moth (*Lymantria dispar* L.), oak decline, and regeneration failures, have furthered interest and concern for its culture and spurred silvicultural research. Consequently, our knowledge of northern red oak has increased substantially in the last decade.

CHARACTERISTICS OF NATURAL STANDS

Composition, Structure, and Yield

Over much of its range, northern red oak is a minor to moderately important component of upland hardwood forests. Stands that are predominantly oak often trace back to the 19th century when grazing and burning of forests

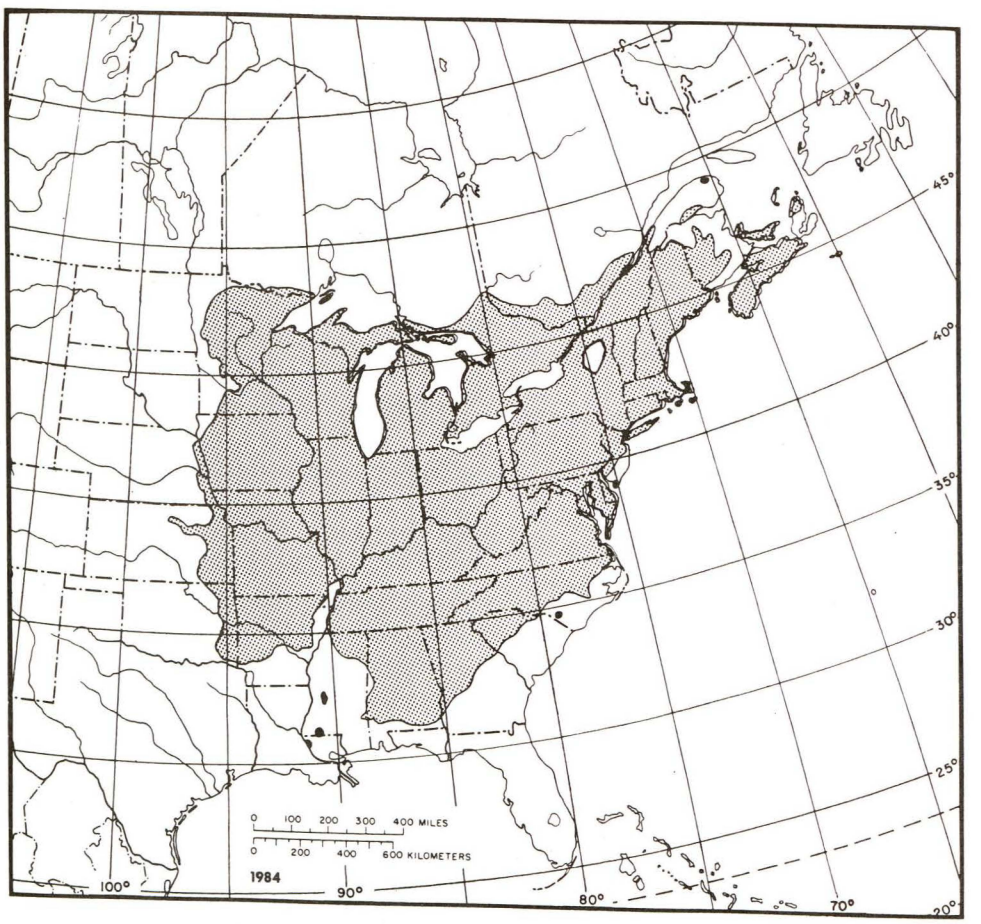

Figure 1.—*The natural range of northern red oak (Sander 1990).*

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were frequent and extensive (Abrams 1992; Grimm 1984; Jokela and Sawtelle 1985; Little 1974; Lorimer 1985, 1989; Nowacki *et al.* 1990). Today, stands dominated by northern red oak are typically even aged and occupy sites ranging from site index 50 to 110.[1] Except during the early stages of stand development, northern red oak is largely restricted to a position of dominance and does not persist in a subordinate crown position (Goff and Zedler 1968, Loftis 1983a). Consequently, in mature stands there typically are few, if any, red oaks of small diameter. When present, trees of subordinate crown classes are usually limited to the more shade tolerant species. In even-aged stands, red oak diameters tend to be normally distributed (Loftis 1983a) by the time stands reach a mean diameter of 8 inches d.b.h. (Gingrich 1967, Hibbs and Bentley 1983). Even in uneven-aged stands of mixed species with an overall inverse J-shaped (negative exponential) diameter distribution, the diameters of the oaks themselves tend to be normally distributed (McGill 1991, Stout 1991).

Mixed oak stands on productive sites, whether even aged or uneven aged, tend to be vertically layered, with one or more lower strata composed of shade tolerant species such as sugar maple (*Acer saccharum* Marsh.), red maple (*A. rubrum* L.), and American beech (*Fagus grandifolia* Ehrh.) (McGill 1991, Nowacki *et al.* 1990, Stout 1991). In some ecosystems, there is a subcanopy of shade tolerant tree species such as flowering dogwood (*Cornus florida* L.) that are incapable of growing into middle or upper crown strata. Several structural layers, including a shrub stratum, in combination with high stand density thus may reduce light intensities on the forest floor to less than 10 percent of full light (Allard 1947, Hanson *et al.* 1987, Pubanz and Lorimer 1992). Under such conditions, northern red oak is typically restricted to one generation because it usually is replaced by more shade tolerant species (Nowacki *et al.* 1990).

Pure northern red oak stands[2] are common in the transition zone between the oak-hickory and mixed mesophytic forests of the Central and Appalachian Hardwood Regions and between the former and northern hardwood forests of the Lake States and New England (Arend and Scholz 1969, Hibbs and Bentley 1983). They also are common in the southern Appalachians, the Driftless Area of southwestern Wisconsin, and contiguous areas in adjacent States. In southwestern Wisconsin, gross yields of normal 100-year-old red oak stands range from about 3,200 cubic feet per acre on site index 50 to 6,200 cubic feet per acre on site index 70 (fig. 2). Diameter growth of northern red oak exceeds that of associated oaks in West Virginia (Trimble 1960). Rotation lengths for sawtimber range from about 80 to 120 years depending on management objectives, site quality, and other factors.

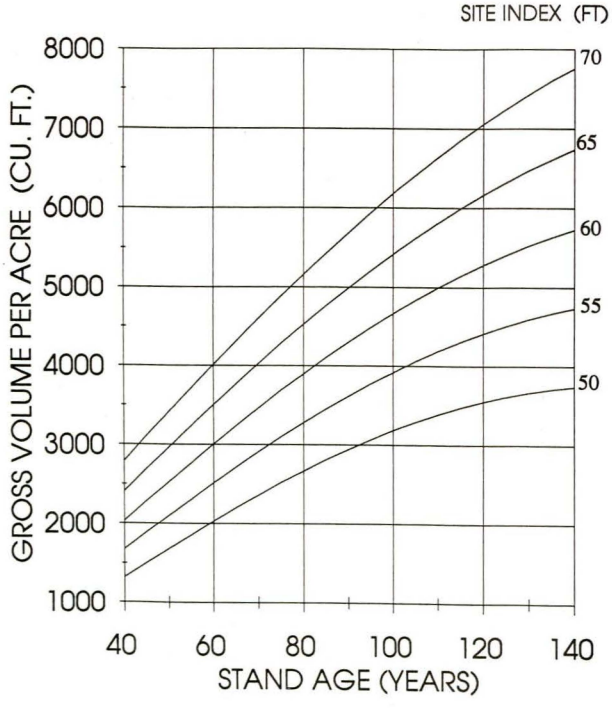

Figure 2.—*Relation of gross volume yield per acre to stand age and site index for stands dominated by northern red oak in southwestern Wisconsin. Includes trees ≥0.6 inches d.b.h., and tops and limbs suitable for cordwood; bark is excluded.* $(V = -249.69(AGE^{.5}) - 0.011636(AGE^{2.5}) + 0.18658(S^2) + 1.2754(SI)(AGE)$, *where V = volume in cubic feet per acre, S = site index (ft), and A = stand age. Adapted from Gevorkiantz and Scholz, 1948 (table 4).)*

[1]*Site index is the mean height in feet of dominant and codominant trees at an index age of 50 years. There is only approximate equivalence among the available sets of site index curves, which are developed by region.*

[2]*A pure stand is herein defined as one in which 80 percent or more of the dominant and codominant trees are of one species.*

Site Index and Site Relations

Site index curves for northern red oak are available for several regions, including the Lake States (Carmean 1978, Gevorkiantz 1957), New England (Hibbs and Bentley 1983), the central Appalachians (Lamson 1980), and the Boston Mountains of Arkansas (Graney 1977). The latter two are composite curves for northern red oak, scarlet oak (*Q. coccinea* Muenchh.), and/or black oak (*Q. velutina* Lam.). There also are composite site index curves for "upland oaks" that, in their development, included northern red oak (e.g., the curves of Olson (1959) for the southeast and Schnur (1937) for the Central States). However, Schnur's curves do not consider potential differences in height growth among species. Because there are differences among the oaks (Carmean 1971, Graney and Bower 1971, Lamson 1980), species-specific curves or curves based on statistically determined species groupings are preferable to curves where such differences have not been considered.

The exceptionally rapid early height growth of red oak stump sprouts raises questions about the applicability of existing site index curves to trees of coppice origin. Currently, there are no site index curves specifically developed for northern red oaks of coppice origin. However, Trimble (1968) concluded that the site index of multiple-stemmed northern red oaks, presumably of coppice origin, and single-stemmed trees of unspecified origin were equal based on Schnur's (1937) curves. Nevertheless, we know that oaks of stump sprout origin grow much faster than those of seedling origin during the first 20 years (Johnson 1975, Zahner *et al.* 1982). The magnitude of related errors in site index estimation is illustrated by a site index comparison of coppice origin trees in mixed oak stands in South Carolina. In that comparison, Olson's (1959) curves estimated a site index at 50 years 18 feet greater than that estimated by curves specifically derived from coppice trees (Zahner *et al.* 1982). It thus would appear prudent not to apply available site index curves for red oak to stands of coppice origin.

There also are equations for estimating the site index of northern red oak from the site index of other species in several regions. In the Lake States, red oak site index can be estimated from the site index of sugar maple, red maple, yellow birch (*Betula alleghaniensis* Britton), paper birch (*B. papyrifera* Marsh.), American basswood (*Tilia americana* L.), American elm (*Ulmus americana* L.), white ash (*Fraxinus americana* L.), and black ash (*F. nigra* Marsh.) (Carmean 1979). In the Southeast, red oak site index can be estimated from the site index of shortleaf pine (*Pinus echinata* Mill.), pitch pine (*P. rigida* Mill.), black oak, white oak (*Quercus alba* L.), southern red oak (*Q. falcata* Michx. var. *falcata*), yellow-poplar (*Liriodendron tulipifera* L.), and sweetgum (*Liquidambar styraciflua* L.) (Doolittle 1958, Nelson and Beaufait 1956, Olson and Della-Bianca 1959). In the Central States, red oak site index can be estimated from the site index of black oak, white oak, scarlet oak, and yellow-poplar (Carmean and Hahn 1983).

Equations for estimating red oak site index from soil and topographic factors also are available for several regions including northwestern West Virginia (Auchmoody and Smith 1979), the Ridge and Valley Region of Pennsylvania (Bowersox and Ward 1972), northeastern Iowa (Einspahr and McComb 1951), the Boston Mountains of Arkansas (Graney 1977), and the northern Appalachians (Trimble and Weitzman 1956, Yawney and Trimble 1968). In general, the relations expressed by those equations show that northern red oak site index, and thus the species' rate of height growth, is greatest on deep soils on north and east aspects and lower slope positions. However, those studies also show that other factors may be associated with site index, including slope shape, soil texture, soil nutrients and pH, thickness of the A_1 horizon, and precipitation. Soil and topographic factors also have been used to define qualitative site productivity classes for oak stands in southern Michigan (Gysel and Arend 1952), and to define a synthetic site quality gradient related to the growth of northern red oak stump sprouts in southern Wisconsin (Johnson 1975).

Ecological classification systems provide another method for assessing northern red oak site relations. The objective of ecological classification is to define vegetation-site (habitat) units within which there is great ecological similarity (Barnes *et al.* 1982). The defined ecological units thus can be used to distinguish among superficially similar red oak stands, e.g., those that belong to the same cover type as defined by Eyre (1980), but which are ecologically very different. Such distinctions are especially useful in assessing regeneration problems. For example, the classification system for Wisconsin developed by Kotar and others (1988) specifies

the relative ease or difficulty of regenerating northern red oak in the habitat types where it commonly occurs. Ecological classification also can be used in red oak stands to specify other important features of each defined ecological unit. These include productivity, characteristic overstory, diameter distributions, value to wildlife, soils, and nutrient cycling relations (Cleland *et al.* 1985, De Geus 1986, Kotar 1991, Zak and Pregitzer 1990).

STAND DENSITY, GROWTH, AND TREE QUALITY

Stocking Guides

Stocking equations and charts derived from them are commonly used as standards for defining and controlling the density of oak stands. Currently available standards express stand density as "stocking percent," a measure of relative stand density (Stout and Larson 1988). Related stocking charts specify the upper and lower limits of absolute measures of stand density (i.e., basal area and numbers of trees per acre) that define the normal range of residual stocking for thinning and other silvicultural operations. The upper and lower levels of this range are called *A* and *B* levels, respectively. *A* level, also called 100 percent stocking, represents stands at average maximum density. *B* level represents the minimum stand density at which trees utilize all the growing space, assuming trees are well distributed. There are stocking charts for the oak-hickory forests of the Central States (Gingrich 1967), and northern red oak forests of New England (Sampson *et al.* 1983) and Wisconsin (McGill *et al.* 1991) (fig. 3).

Stocking percent provides a better measure of the degree of tree crowding than basal area alone because large trees require less space, proportionate to their basal area, than small trees. Thus, for a given basal area per acre, stands comprised of large trees are at a lower stocking percent, i.e., are less crowded, than stands comprised of small trees (fig. 3). The application, derivation, advantages, and limitations of stocking concepts have been discussed in more detail by others (e.g., Ernst and Knapp 1985, Gingrich 1967, Leak 1981, Leary and Stansfield 1986, Stout and Larson 1988).

Intermediate Cuttings

Not everybody agrees on how and when intermediate cuttings should be made in red oak stands. However, silviculturists generally concede that stands originating from seedlings should be treated differently from those originating primarily from stump sprouts. The latter require early intermediate cuttings if tree quality matters. The former may benefit from no thinning for 40 years or longer (Carvell 1971).

In central New England, red oak commonly occurs in association with red maple and birch (*Betula* spp.), where site index ranges from about 55 to 75 (Hibbs and Bentley 1983, Oliver 1978, 1980). Although red maple and birch typically outnumber and outgrow the oaks during the first 2 decades of stand life, red oak ultimately emerges to form the dominant canopy because of its greater survival rate and its sustained growth rate (Hibbs 1981, Oliver 1978). Only about twice the number of red oak crop trees needed at the end of the rotation are needed at stand age 25 for the stand to be considered adequately stocked with red oak (Hibbs 1981). Recommendations thus are to delay first thinnings to stand age 45 (Hibbs and Bentley 1983, 1984). During the first 45 years, rapid height growth and the development of long, branchless boles are encouraged by maintaining high stand densities. Length of clear bole largely depends on early stem development and site quality (Carmean and Boyce 1973).

Although early thinning increases diameter growth, studies in New England have shown that merchantable height is reduced (Hibbs and Bentley 1984). The resulting value lost related to reduced merchantable height is not compensated by the gain in diameter. After stand age 45, recommendations are to reduce stand density to *B*-level stocking every 10 years until shelterwood cuttings are made to encourage the development of oak reproduction (Hibbs and Bentley 1983, Sampson *et al.* 1983). The recommended rotation, assuming current utilization technology, is about 95 years when diameters of individual trees reach financial maturity at 21 to 25 inches d.b.h., depending on site quality (Hibbs and Bentley 1984).

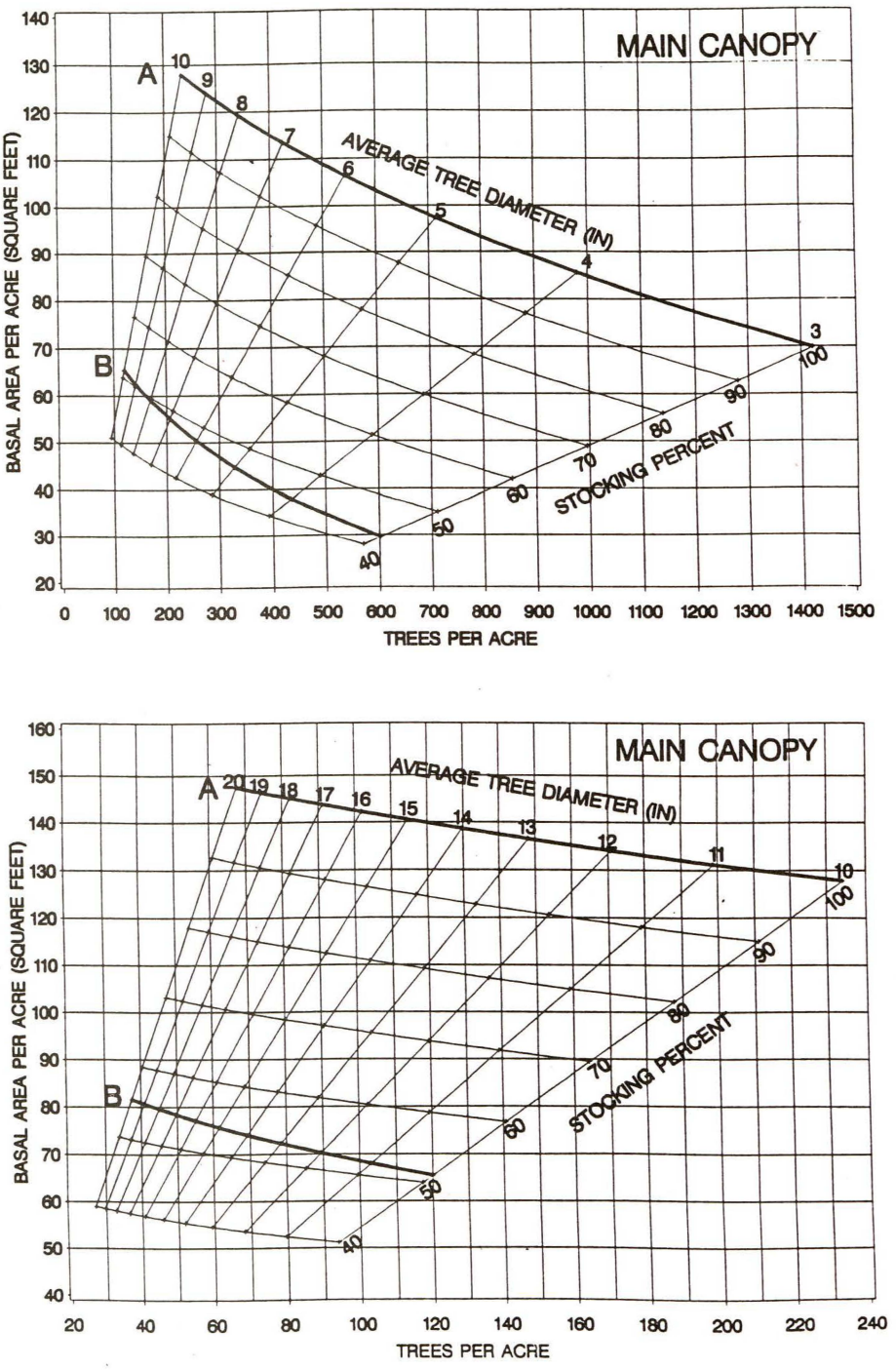

Figure 3.—*Relation of basal area, number of trees, and average tree diameter to stocking percent in stands dominated by northern red oak in Wisconsin. (The charts represent stocking of trees in the main canopy (intermediate, codominant, and dominant crown classes) for average tree diameters of 3 to 10 inches (upper figure) and 10 to 20 inches (lower figure). The area between curves* A *and* B *represents the range of stocking where main canopy trees fully utilize growing space. The* A *(100 percent) curve defines stands at average maximum (normal) density. Average tree diameter is the diameter of the tree of average basal area for trees ≥0.6 inches d.b.h. From McGill* et al. *1991.)*

Where northern red oaks are overtopped by long-lived competitors early in the rotation, early release may be necessary if the oaks are to attain dominance. This is especially true where red oak site index is greater than 70 and where the species must share dominance with sugar maple, American beech, yellow-poplar, black cherry (*Prunus serotina* Ehrh.), or other long-lived species. Where red oak is not overtopped, recommendations are to defer thinning until crop trees are at least 25 feet tall (Lamson and Smith 1978). In West Virginia, removing competitors within a 5-foot radius of 9-year-old crop trees on site index 70 did not significantly increase height or diameter growth or length of clear stem, and it did not prevent crown-class regression during the 5-year study period (Lamson and Smith 1978). Similar results were observed on site index 60 for 7-year-old trees (Trimble 1974). If thinning in young stands is undertaken, recommendations are to do so conservatively by creating canopy gaps no more than 5 feet wide on three or four sides of selected crop trees (Sampson *et al.* 1983).

Besides controlling composition, early thinnings also increase yields. Studies in the central hardwood region show that cubic-foot yields of oak stands are more than 50 percent greater when thinning (cleaning) is begun at age 10 than when thinning is begun at age 60 (Gingrich 1971). Although economic considerations may preclude cleanings, oak stands often can be profitably thinned as early as stand age 25 where there is a market for fuelwood or pulpwood (Carvell 1971). Stands should not be thinned after they reach about 60 years (Sander 1977).

Even though maximum yields may occur at stocking levels below *B* level (Dale 1972, Leak 1981), the lower limit of thinning is usually set at *B* level to ensure bole quality (Dale and Sonderman 1984). Thinning below *B* level risks increasing epicormic branching on the lower bole with consequent loss of tree value. However, stocking levels after thinning do not have a significant effect on the stem form of oaks (Hilt and Dale 1979).

Thinning within clumps of northern red oak stump sprouts in Wisconsin maximizes residual stem growth and quality when clumps are thinned to one stem before they reach 3 inches d.b.h. (age 12 to 15) (Johnson and Rogers 1984). Growth simulations indicate that thinning clumps to one stem at age 5 on site index 70 can produce boles 11.6 inches d.b.h. at age 25 when coupled with periodic thinnings around crop stems to a spacing that approximates *B*-level stocking (table 1). Recommendations are to thin clumps only on site index 65 or greater.

Clump thinning recommendations based on a West Virginia study (Lamson 1988) are: (1) to thin clumps when they are 10 to 20 years old, and only on good sites; (2) to select crop stems that are dominant or codominant, straight, and free of forks and other defects in the lower 17-foot bole, and that originate not more than 6 inches above groundline;[3] (3) to retain only the best one or two crop stems per clump. If two crop stems are retained, the stems should be far enough apart so that during their expected life span they do not fuse together at a common base (Roth 1956, Stroempl 1983); (4) to remove all intermediate and codominant trees if their crowns touch the crop stem crown, or if their crowns are above or below the crop stem crown; and (5) to thin around thinned clumps in about 10 years to sustain maximum diameter growth. Because pruning 12-year-old northern red oak stump sprouts reduced 10-year diameter increment, that practice is not recommended in young stands (Lamson 1988).[4]

Several individual-tree-based growth models are available for projecting growth and yield and for simulating forest management practices in northern red oak stands (Fairweather 1988, Hibbs and Bentley 1984, Hilt and Teck 1988, Johnson and Rogers 1984, Shifley 1987).

Gypsy Moth and Oak Decline

Among the several agents that pose serious threats to the health and longevity of northern red oak, the gypsy moth and oak decline probably present the most severe problems. In the eastern half of the species' range, defoliation from the gypsy moth is a major concern. Oaks

[3] *The author recommends selecting only stems originating within 1 inch of ground line to minimize risks related to decay transmission from stumps and mortality related to weak attachment of sprouts to stump.*

[4] *Trees were pruned to a height not exceeding 75 percent of their total height or more than 25 feet.*

Table 1.—*Estimated 25th-year diameters of northern red oak stump sprouts in thinned and unthinned sprout clumps on good sites (site index 70) in Wisconsin*[a]

Initial stem d.b.h. (inches)	Age of sprouts when initially thinned or observed (years)							
	5		10		15		20	
	Thinned to 1 stem	Unthinned[b]	Thinned to 1 stem	Unthinned	Thinned to 1 stem	Unthinned	Thinned to 1 stem	Unthinned
	Estimated 25th-year d.b.h. (inches)							
0.5	10.6	4.7						
1.0	10.8	6.5	8.5	4.4				
1.5	11.2	8.4	8.8	5.6	6.5	3.8	4.2	2.5
2.0	11.6	10.0	9.1	6.7	6.9	4.6	4.6	3.1
2.5			9.5	7.8	7.2	5.3	5.0	3.7
3.0			10.0	8.6	7.7	6.1	5.4	4.3
3.5			10.5	9.6	8.1	6.6	5.8	4.9
4.0					8.6	7.6	6.3	5.5
4.5					9.1	8.5	6.6	6.1
5.0							7.2	6.6
5.5							7.7	7.2
6.0							8.2	7.8
6.5							8.7	8.4
7.0							9.2	8.9
7.5							9.8	9.5
8.0							10.3	10.1

[a] *From Johnson and Rogers (1980).*

[b] *In unthinned clumps, estimates depend on the ratio of the basal area of the crop stem to total clump basal area (relative basal area). The values shown thus are based on the mean trend of relative basal area for a given initial crop stem diameter and age.*

are the preferred host, and thus the stands most susceptible to attack are those with a high proportion of oaks (Gottschalk 1991). However, northern red oak ranks behind chestnut oak (*Quercus prinus* L.), black oak, and scarlet oak as a preferred host (Gansner and Herrick 1985). In all species, heavy defoliation may cause trees to refoliate during the same year, which in turn may deplete carbohydrate reserves and lead to attack by secondary organisms such as shoestring root rot (*Armillaria* spp.) and twolined chestnut borer (*Agrilus bilineatus*) (Gansner and Herrick 1985, Gottschalk *et al.* 1989). Trees at highest risk are those in suppressed (overtopped) and intermediate crown classes and, within a given crown class, trees with low-vigor crowns (Herrick and Gansner 1987). Mortality associated with gypsy moth defoliation also is greater on good sites than on poor sites (Gansner 1987), and under some conditions is greater in thinned stands than in unthinned stands (Twery and Gottschalk 1989).

The most significant effect of the gypsy moth on the oak resource is not mortality, but reduced growth, yield, and wood quality. Gypsy moth outbreaks occur at 7- to 10-year intervals and last 1 to 2 years (Gottschalk *et al.* 1989). It may take 3 years for stand growth to recover from a single defoliation (Twery 1987). For two defoliations in 1 decade, loss of volume increment has been estimated at about 10 percent, exclusive of mortality. For two defoliations per 5 years, estimated growth losses are about 19 percent (Twery 1987). However, such losses may be offset by subsequent gains in growth of the survivors related to the thinning effect from mortality. To minimize loss in value of sawtimber-size oaks killed by defoliation, trees should be salvaged within the first year after death (Garges *et al.* 1984).

Strategies for reducing timber losses from gypsy moth include reducing the proportion of oaks in the stand, applying insecticides, and removing trees that are preferred hosts and refuges for the insect. The latter include oaks and other species in poor crown condition. Specific strategies and options for coping with the gypsy moth are varied and depend on stand condition and age, the current status of the insect in the stand, and management objectives (Gottschalk 1987, 1988, 1989, 1991, 1993).

Oak decline, whose effects on oaks range from partial crown dieback to tree death, also afflicts northern red oak. This phenomenon is believed to be initiated by drought stress and/or defoliation, which is subsequently exacerbated by further insect and disease attack (Wargo and Haack 1991). Maintaining species diversity is believed to be important in minimizing the impact of this stress-mediated disease (Houston 1987). Stands at greatest risk are older stands containing a large proportion of trees in the red oak group (subgenus *Erythrobalanus*) that occur on xeric sites (red oak site index <70) (Starkey *et al.* 1989). Because tree age and site quality are the most important factors that predispose oaks to decline, the ratio of site index to tree or stand age is a useful index of their vulnerability to decline; low ratios are associated with a high incidence of decline (Oak and Starkey 1991).

Global warming and associated summer drought and winter freeze-thaw cycles also have been implicated in the increased occurrence of dieback and decline of forest trees across North America (Auclair *et al.* 1990). Although oaks are known for their great drought tolerance, recent research has shown that, to the contrary, they are vulnerable to sudden and fatal disruptions in xylem water conduction (embolisms) induced by water stress, especially stress caused by winter desiccation (Cochard and Tyree 1990). Those effects eventually may fit into a more comprehensive and fundamental decline theory than those currently proposed (*cf.* Ammon *et al.* 1992, Auclair *et al.* 1992, Houston 1992, Manion and Lachance 1992, Mueller-Dombois 1992, Wargo and Haack 1991).

Although much remains to be learned about oak decline, possible preventive or remedial silvicultural treatments include: (1) thinning early to reduce future competition-induced stress and to favor less susceptible species, (2) reducing rotation age, (3) favoring less susceptible species when regenerating stands, and (4) controlling defoliating insects (Starkey *et al.* 1989). There is some evidence that making partial cuttings in stands where decline is already present increase the severity of decline. Possible explanations include an increased food supply for shoestring root rot originating from root systems of stumps and trees injured during logging, reduced soil moisture related to soil compaction from logging, and increased temperatures on the forest floor related to reduced overstory density (Starkey *et al.* 1989). Because highest mortality of oaks from decline occurs on droughty sites, populations of northern red oak may be affected less than the more xerophytic oaks such as black oak and scarlet oak. Nevertheless, a high incidence of decline in northern red oak has been observed in some areas of the southern Appalachians (Tainter *et al.* 1984).

REGENERATION ECOLOGY

Acorn Production

Regeneration is probably the least well understood facet of northern red oak silviculture (Crow 1988). One reason for this is the unpredictable occurrence of acorn crops (Cecich 1991). Acorn production varies greatly from year to year and from tree to tree. Results from one study indicate that tree-to-tree variation is significantly greater than the former (Tryon and Carvell 1962). Studies of other oak species indicate that tree-to-tree variation in acorn production is under strong genetic control (Farmer 1981, Wolgast 1972). Some trees never produce acorns, even when environmental conditions are apparently favorable (Sharp 1958). In contrast, year-to-year variation in acorn production apparently is the result of the combined effects of inherited and other factors such as weather and insects (Christisen and Kearby 1984, Sharp and Sprague 1967). In some species, notably those in the white oak (*Lepidobalanus)* subgenus, seed production tends to be periodic in the absence of adverse weather. During those times, acorn crops generally occur every other year and good crops occur about once every 4 years (Beck 1977, Christisen and Kearby 1984, Downs and McQuilkin 1944, Goodrum *et al.* 1971, Myers 1978). Periodicity in the white oaks is also synchronized, with all fruitful trees within a species, locale, and year producing at their inherent individual, but often environmentally constrained, capacity (Sharp 1958, Myers 1978).

In contrast, evidence for periodicity in acorn production of northern red oak is more obscure. Within a local population of trees, acorn production apparently is not synchronized, i.e., not all inherently fruitful trees bear acorns the same year. Among 10 open-grown trees observed for 9 years in central Pennsylvania, nine produced acorns each year but not equally (Sharp 1958). Of those nine trees, one-third produced heavy acorn crops each year, but no individual tree

produced a heavy crop in consecutive years. In the southern Appalachians, northern red oak tended to produce above-average or "bumper" acorn crops at 5-year intervals during a 12-year study, with 2 years of failure and 2 years of moderate yields in intervening years (Beck 1977). In northeastern Wisconsin, bumper crops occurred on the average at 7-year intervals during a 21-year study. But some bumper crops occurred as few as 2 years apart (Godman and Mattson 1976). Those observations tend to support the view that there is less year-to-year variation in acorn production within a local population of northern red oaks than within a local population of white oaks (Tryon and Carvell 1962). From a silvicultural perspective, inherent variation in acorn production and apparent sensitivity of flowering and fruiting to unpredictable weather events represent essentially random elements in the prediction of seedling establishment. The problem is further confounded by damage to acorns from insects, fungi, freezing, and consumption by birds and mammals (Beck 1977, Christisen and Kearby 1984, Downs and McQuilkin 1944, Goodrum *et al.* 1971, Korstian 1927, Krajicek 1960, Marquis *et al.* 1976, McGee 1988, Mignery 1975, Myers 1978, Olson and Boyce 1971, Scholz 1964, Sluder *et al.* 1961, Tryon and Carvell 1962). Despite the numerous confounding factors, there nevertheless is evidence that inherent periodicity in red oak acorn production occurs at 4-year intervals (Sork *et al.* 1993).

Downs and McQuilkin (1944) observed acorn production of dominant and codominant northern red and other oaks by diameter classes in southern Appalachian stands. Based on 7 years of observations, their sample of 42 red oaks showed that annual acorn production peaked in trees 20 to 22 inches d.b.h. (fig. 4).[5] The acorn producing capacity of an oak stand, and correlatively the rate of seedling input, thus changes with stand size and age. Neither young trees nor old senescent trees produce large acorn crops.

For oaks of a given inherent acorn-producing capacity, those growing in the open produce more acorns than those growing in closed-

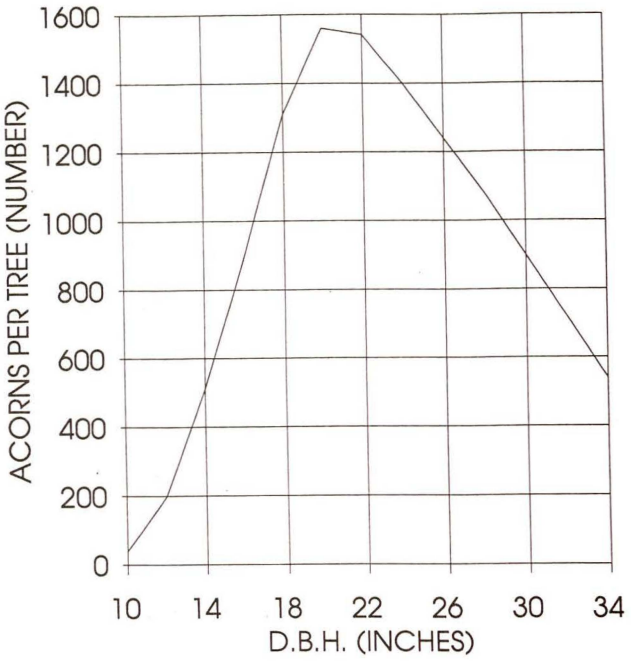

Figure 4.—*Annual production of northern red oak acorns averaged over 7 years in the southern Appalachians in relation to tree diameter (adapted from Downs 1944).*

canopy forests (Sharp 1958, Sharp and Sprague 1967). Exposed crown areas of northern red oaks in Michigan produced five times more acorns per unit of crown area than shaded crown areas (Verme 1953). We might therefore expect some of the variation in acorn-producing potential among trees to be related to variation in stand density. Stocking, a relative measure of stand density, can vary greatly even among stands with closed canopies, i.e., canopies above *B*-level stocking (fig. 3). As stocking increases, the average area of individual tree crowns decreases, which in turn reduces the average acorn production per tree.

Thinning and consequent crown expansion thus have the potential to increase acorn production, especially if good seed producers are reserved. The positive effects from thinning also increase the likelihood that oaks in the residual stand will survive gypsy moth defoliation and thus recover acorn production after outbreaks of the insect have subsided. Nevertheless, even moderate defoliation can reduce acorn production, and severe defoliation may cause nearly complete loss of production (Gottschalk 1989). Reducing stand density also has the potential to reduce acorn production if many of the good acorn producers are inadvertently cut in the

[5]*However, 70 percent of trees 22 inches d.b.h. and larger (20 trees) that Downs and McQuilkin sampled were categorized as "overmature and decadent" (data on file, Southeastern Forest Experiment Station, Asheville, NC).*

process. However, this problem can be largely averted by thinning from below, which concentrates removals on the smaller trees that are unlikely to be significant acorn producers.

Seedlings and Seedling Sprouts

Large numbers of new red oak seedlings occur as unpredictable population waves associated with bumper acorn crops. Seedling growth and survival in the understory are subsequently influenced by light, soil moisture, nutrients, and other factors. Reducing overhead shade can increase light intensity and thereby increase seedling survival and growth (Beck 1970; Crow 1992; Loftis 1988, 1990a). But small trees, shrubs, and ground cover also can effectively reduce light levels at seedling height (Beck 1970, Loftis 1990a, Scholz 1955). Variation in those factors are associated with 5-year seedling survival ranging from less than 20 percent to more than 80 percent (fig. 5). Other factors that can reduce oak seedling survival and growth include animal browsing, insect defoliation, drought, and frost (Crow 1992, Gottschalk 1988, Hanson *et al.* 1987, Korstian 1927, McGee 1988). Moreover, the microsites that favor initial establishment of oak seedlings may not favor their persistence (Harrison and Werner 1984). Cool, moist northeast-facing slopes favor initial seedling establishment, while the more southerly or neutral slopes, where competition is less intense and light levels are higher, favor long-term survival and growth and thus the accumulation of reproduction (Carvell and Tryon 1961, Sander *et al.* 1984, Walters 1990).

In the drier ecosystems, populations of oak seedlings and seedling sprouts may accumulate over several acorn crops. This accumulation is one of the most important aspects of the regeneration ecology of oaks. Silviculturists call this "advance reproduction" because, in the even-aged management of oaks, it is present in advance of final harvest. Its presence and development largely determine the importance of oaks after natural or human-caused events destroy or remove the parent stand. Successful regeneration of oaks thus largely depends on an accumulated population of advance reproduction that can rapidly capture growing space after stand disturbances. Whether the overstory is removed in small groups or over large areas, the resulting spatial units of reproduction are even aged. Although oaks generally are not recognized as species well adapted to capturing small canopy gaps (Crow 1988, Ehrenfeld 1980), they have the potential to do so if advance reproduction of sufficient size is present. For example, 10-foot-tall northern red oak advance reproduction captured canopy gaps of one-twentieth acre in a southern Wisconsin maple/oak stand (Lorimer 1983).

Although red oak reproduction may accumulate over successive acorn crops in xeric ecosystems, it is not as physiologically adapted there as black oak, white oak, scarlet oak, chestnut oak, and other xerophytic oaks and tree species (Abrams 1990, Bourdeau 1954, Wuenscher and Kozlowski 1971). Red oak therefore is usually a minor component of those ecosystems. Reproduction of the more xerophytic oaks nevertheless may accumulate in the understory for decades (Merz and Boyce 1956) because of its drought tolerance and a favorable light environment (Abrams 1990, Bourdeau 1954). This "auto-accumulation" of oak reproduction on the drier sites occurs throughout the Eastern United States (Johnson 1993). Much of the lore of oak regeneration is derived from studies and observations made in such ecosystems.

Oak seedlings become seedling sprouts after dying back and resprouting one or more times. Dieback and resprouting are important processes in the life of oak reproduction in the drier ecosystems because they facilitate the development of large root:shoot ratios and root mass, which in turn effect rapid shoot growth after the overstory is harvested or destroyed by natural forces (Johnson 1979, Sander 1971). The xerophytic oaks may require two or more decades in the understory before they develop the root mass necessary for competitive shoot growth after overstory removal (Merz and Boyce 1956; Sander 1971, 1979; Sander and Clark 1971).

In mesic ecosystems, the density of northern red oak advance reproduction fluctuates widely, even where the species dominates the overstory (Carvell and Tryon 1961, Curtis 1959, Will-Wolf 1991). Abundant red oak reproduction is often attributable to a single acorn crop (cohort). Because of low survival rates, most seedlings within a single cohort may die before the next good acorn crop occurs. The rapid rate of seedling disappearance largely results from red oak's intolerance of shade and low light levels on the forest floor (Crow 1992, Hanson *et al.* 1987). Low light levels, in turn, are caused by the high

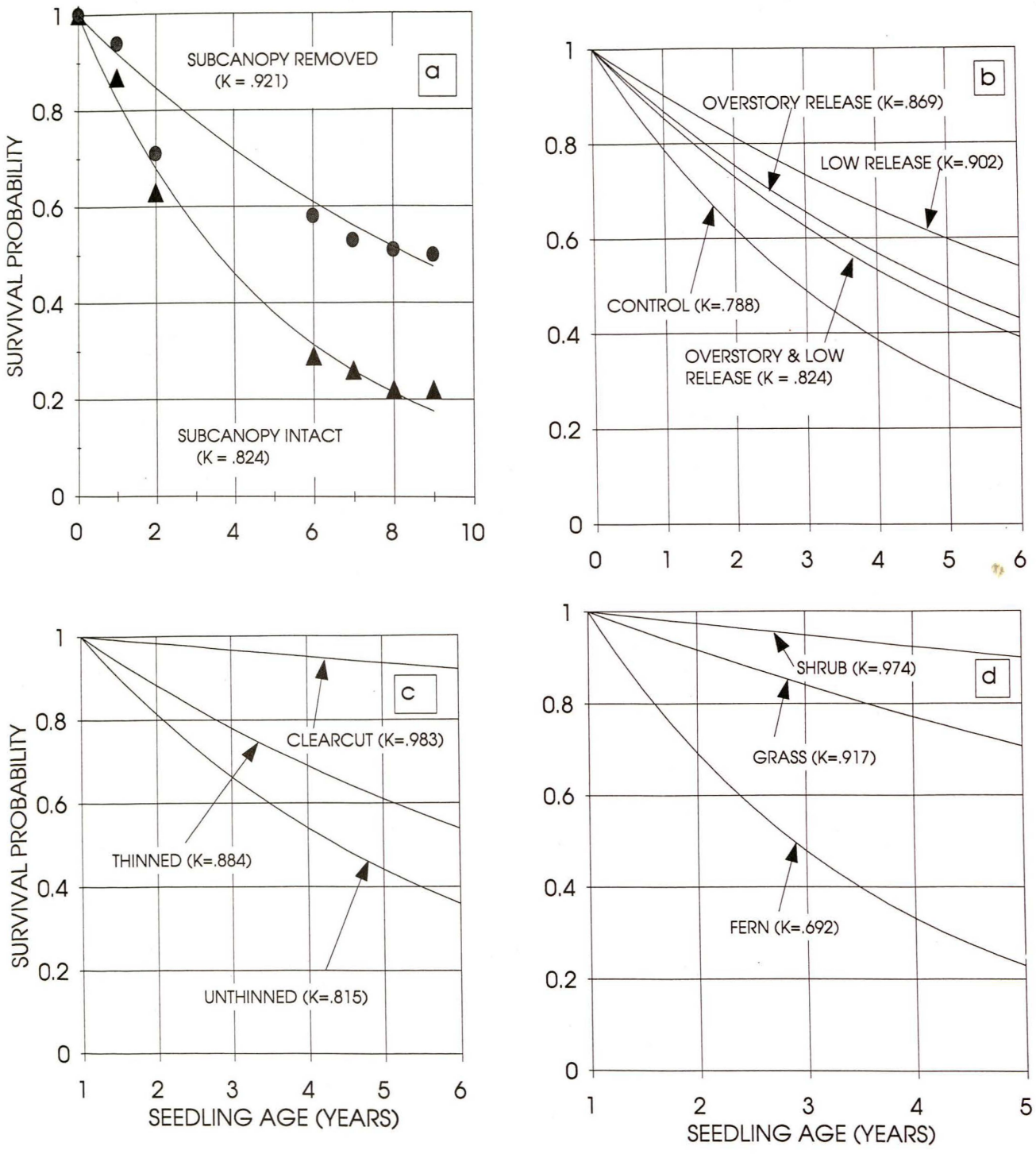

Figure 5.—*Survival curves for northern red oak seedlings originating from single acorn crops (cohorts). (a) Under shelterwoods with and without a subcanopy of small trees in mesic forests in North Carolina (adapted from Loftis 1988); (b) In four overstory/understory release treatments in mesic forests in North Carolina (adapted from Beck 1970); (c) In clearcut, thinned, and unthinned stands treated with an herbicide in dry-mesic forests in northeastern Wisconsin (adapted from Crow 1992); and (d) Competing with three classes of ground cover under fully stocked mesic forests in southwestern Wisconsin (adapted from Scholz 1955). (Survival is expressed as a negative exponential annual survival rate (K), from age 0 (germination) or age 1 year. Survival probability (P) = K^y, where y = years since initial population census, i.e., years since P = 1.)*

overstory basal areas and multiple subcanopy layers that characterize most northern red oak stands (Auclair and Cottam 1971, Braun 1967, Loftis 1990b, McGill 1991). Under those conditions, the species is usually limited to one generation as a major stand dominant because the light environment does not favor the buildup of red oak advance reproduction.

Northern red oak reproduction therefore is at a competitive disadvantage in mesic ecosystems. Before overstory removal, it must grow under deep shade and in competition with shade tolerant species; and after overstory removal, it must grow with a myriad of preestablished tree reproduction, fast-growing intolerant species originating from seed, stump sprouts, and other competition (Beck and Hooper 1986, Crow 1988, Loftis 1983b). The enigma of northern red oak thus is its exclusion from the xeric ecosystems because of its drought intolerance, and from the mesic ecosystems because of its shade intolerance. In the absence of silvicultural intervention, this leaves relatively narrow "windows of opportunity" for northern red oak to regenerate itself. Some of these windows result from the auto-accumulation of red oak reproduction that is intrinsic to some dry-mesic ecosystems. Elsewhere they may result from disturbances caused by humans or other external forces that, by design or accident, result in reduced competition, increased light, and the accumulation of reproduction.

However, it is not by chance that northern red oak exerts its greatest influence in the more mesic ecosystems. Although less efficient at coping with water stress than its xerophytic associates (Wuenscher and Kozlowski 1971), red oak is more shade tolerant (Curtis 1959, Sander 1990). Also, where conditions are favorable, red oak seedlings have the capacity for rapid growth (Farmer 1975, 1980) that is less dependent on the presence of a large root system than the more xerophytic oaks. Moreover, the basic site resources required to effect this growth—nutrients and soil moisture—are available in the mesic ecosystems. So, where light is not a limiting factor, the long regeneration establishment periods of a decade or more required by the dry-site oaks may not be necessary (Jacobs and Wray 1992, Johnson *et al.* 1989). The silvicultural challenge in mesic ecosystems is to modify the light and competition environment so that the establishment and growth potential of red oak reproduction can be realized.

Stump Sprouts

Stump sprouts arise from the stumps of harvested overstory trees.[6] They are an acceptable form of oak reproduction with minimal decay risk when they originate within 1 inch of groundline (Roth and Hepting 1969). In West Virginia, Lamson (1976) found that more than 80 percent of 8- and 12-year-old unthinned sprout clumps of northern red oak contained at least one potential crop stem. Estimated numbers of stumps that produce sprouts can be used to compensate for deficiencies in the regeneration potential of oak advance reproduction (Loftis 1990a, Sander *et al.* 1984). In Wisconsin clearcuts, the percentage of 70- to 120-year-old harvested red oaks with stump sprouts ranged from 56 to 1 percent for trees from 8 to 26 inches d.b.h., respectively (fig. 6). However, there was no apparent relation between frequency of sprouting and parent tree diameter in West Virginia where 93 percent of 50- to 60-year-old trees sprouted (Wendel 1975). Those differences suggest that sprouting in northern red oak is determined by both parent tree size and age, similar to that observed in white oak and black oak (Johnson 1977). Because of their rapid height growth and high survival rates, a large proportion of stump sprouts attain early dominance and maintain that crown position (Johnson 1975, Johnson and Rogers 1984, Sander *et al.* 1984). Nevertheless, contributions to stocking from red oak stump sprouts will be a minor source of reproduction in stands managed on 90-year or longer rotations, even in pure stands. Stump sprouting also may be reduced in trees weakened by gypsy moth defoliation and oak decline (Gottschalk 1988, Oak *et al.* 1988).

REGENERATION METHODS

Natural Regeneration

The clearcutting method

Clearcutting has been widely used to regenerate oaks in the relatively xeric oak-hickory forests of the Central States and elsewhere where oak advance reproduction auto-accumulates (Johnson 1993, Roach and Gingrich 1968,

[6] *Although the definition of overstory varies, it refers here to trees ≥1.6 inches d.b.h. (Gingrich 1967) or ≥2 inches in ground line diameter (Sander and Clark 1971).*

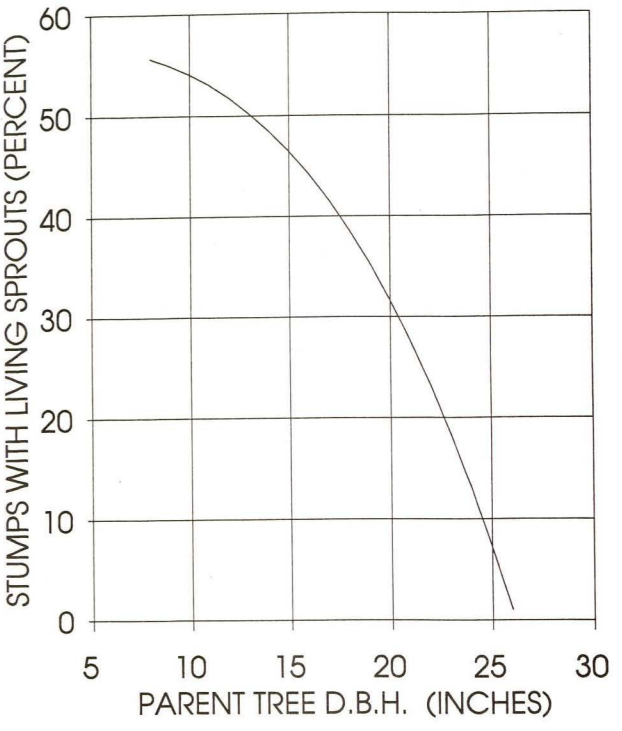

Figure 6.—*Percent of northern red oak stumps with sprouts in 4- to 23-year-old clearcuts in Wisconsin in relation to parent tree d.b.h. (Sprouting percent = 57.3 - 0.0032(D.B.H.).*[3] *Ages of parent trees range from approximately 70 to 120 years. From Johnson 1975.)*

Sander 1977). However, northern red oak is unlikely to be a major component of those stands because it is not as well adapted to dry sites as the more xerophytic oaks (Wuenscher and Kozlowski 1971). But red oak is often important in the dry-mesic segment of the moisture gradient, i.e., sites that are neither extremely xeric nor mesic (Curtis 1959, Nowacki *et al.* 1990). In those ecosystems, the accumulation of red oak reproduction may be sufficient for stand replacement after clearcutting. The success of the method usually depends on a long reproduction establishment period lasting a decade or longer (Sander 1971, 1977; Scholz 1952). For some regions, there are guidelines for evaluating the regeneration potential of oak stands before they are clearcut (Loftis 1990b, Marquis *et al.* 1984, Sander *et al. 1984).*

In the more mesic ecosystems, clearcutting generally has not been successful in regenerating northern red oak (Johnson 1976, Loftis 1988, McGee and Hooper 1975). Clearcutting, by itself, usually accelerates succession toward shade-tolerant hardwoods on those sites (Abrams and Nowacki 1992). Even when there is abundant red oak advance reproduction, it is usually suppressed by the growth of non-oak sprouts and other competition after overstory removal (Beck 1970, McGee and Hooper 1975). Exceptions may occur where a large proportion of overstory red oaks sprout (Johnson 1975, Wendel 1975), or where competition is not severe or is controlled (Jacobs and Wray 1992, Johnson *et al.* 1989).

Alternatives to the "reproduction accumulation" model for regenerating red oak by clearcutting have been proposed for the Driftless Area of southwestern Wisconsin and adjacent States (Bundy *et al.* 1991, Jacobs and Wray 1992, Johnson *et al.* 1989). There, the site index of red oak in the more mesic ecosystems typically ranges from 65 to 70 (Gevorkiantz 1957, Gevorkiantz and Scholz 1948). On those sites, thousands of red oak seedlings per acre may become established in a single year following a good acorn crop (Johnson 1974, Scholz 1955). Moreover, those numbers can be increased by mechanical soil scarification (Scholz 1955). Scarification also can reduce competition and thus increase the growth of red oak seedlings (Bundy *et al.* 1991). After overstory removal, the growth of red oak reproduction on productive sites can be rapid (Farmer 1975, 1980) and less dependent on the development of a large root system and a long establishment period than the more xerophytic oaks. Thus, large numbers of red oak seedlings and a favorable post-harvest growth environment can combine to effect successful regeneration even when the probability of an individual seedling surviving to attain dominance is relatively small. Unlike stands in many other mesic ecosystems, the density of competing trees in Driftless Area stands is relatively low and often comprised of species such as black cherry, paper birch (*Betula papyrifera* Marsh.), elms (*Ulmus* spp.), and hickories (*Carya* spp.) (Johnson 1976, Martin *et al.* 1992). After clearcutting, the rapid dropout rates of those species from the main canopy are similar to the non-oaks in young red oak stands in New England (Hibbs and Bentley 1984, Johnson 1976, Oliver 1978).

Soil scarification has been used in the Driftless Area to effectively reduce competition and simultaneously prepare a patchy seedbed of mineral soil (Bundy *et al.* 1991, Jacobs and

Wray 1992). One technique involves the use of a tractor blade set 6 inches above ground during a good acorn crop. The treatment results in mechanical breakage of low vegetation, including tree reproduction and shrubs, while simultaneously affecting only moderate soil disturbance. In one trial, the method increased the height and leaf area of red oak reproduction two growing seasons after treatment (1 year after clearcutting) (Bundy *et al.* 1991). A similar treatment that consists of mechanical uprooting of low vegetation during logging, or in a separate operation before or after logging, also has been proposed (Jacobs and Wray 1992). Experience has shown that oak advance reproduction survives the treatment because of its deep tap root and capacity for sprouting after top injury. The recommended time to apply the treatment is in the fall during a good seed year before acorns drop. Timing the treatment with acorn fall can increase numbers of seedlings as well as reduce competition. Applying herbicides to the understory before clearcutting and concurrently with a good acorn crop also can facilitate regeneration of red oak. Even though the herbicide kills the oak advance reproduction, one trial resulted in about 1,000 red oak stems per acre 0.5 inches d.b.h. and larger 11 years after clearcutting; about 27 percent were codominant or larger (Johnson *et al.* 1989). Strategies for regenerating northern red oak in the Driftless Area are discussed in more detail by Jacobs and Wray (1992).

In New England and the Lake States, northern red oak sometimes regenerates under pine stands if there is a nearby red oak seed source (Cline and Lockard 1925, Crow and Isebrands 1985). When the pine is harvested, the oak advance reproduction then may capture the site (Sampson *et al.* 1983). Such pine-to-oak successions may be facilitated by the dispersal of acorns by animals. Small mammals disperse red oak acorns up to about 60 feet (Sork 1984), and blue jays (*Cyanocitta cristata*) disperse them up to 2.5 miles (Johnson and Adkisson 1986). Although most dispersed acorns are consumed, even the small surviving proportion of blue jay-dispersed acorns can produce significant numbers of oak seedlings because of the large numbers of acorns that are dispersed and the favorable germination and growth environments they are dispersed to (Johnson and Webb 1989).

The shelterwood method

Probably the most frequently cited method for regenerating oaks is the shelterwood method (Beck 1991, Hannah 1987, Jacobs and Wray 1992, Korstian 1927, Sampson *et al.* 1983, Sander 1979, Scholz 1952, Smith 1986). The method is potentially suited to regenerating northern red oak where the species most frequently occurs—in the troublesome mesic ecosystems where it is difficult to obtain the accumulation and development of oak advance reproduction. The essential feature of the shelterwood method is a reduction in stand density in one or more steps near the end of the rotation to encourage establishment and/or growth of reproduction (Smith 1986). Normally, the final overstory removal is made when established reproduction is deemed adequate for replacing the parent stand. The shelterwood can even be maintained until a two-aged, or "irregular," shelterwood develops (Beck 1991, Smith 1986).

Although the shelterwood method has not always been successful in regenerating northern red oak (Martin and Hix 1988, Walters 1990), when effectively applied it provides the light required for the growth of reproduction without stimulating the competition. In mesic ecosystems, successful application of the method also requires coordinating overstory density control with competition control and, in some cases, acorn production. Moreover, the required timing and intensity of those operations and the length of the shelterwood period may vary among ecosystems.

Relative light intensities under unthinned hardwood stands range from about 1 to 10 percent of that in the open (Allard 1947, Gatherum 1961, Gottschalk 1985, Hanson *et al.* 1987, Pubanz and Lorimer 1992). At the lower end of that range, light is insufficient to sustain rates of photosynthesis that counterbalance losses to respiration in northern red oak seedlings (Hanson *et al.* 1987). Nevertheless, red oak seedlings require only a moderate amount of light. Gottschalk (1985) reported maximum height and diameter growth of red oak seedlings at all relative light intensities above 20 percent. A light intensity 15 percent of that in a new clearcut was observed under an oak shelterwood in Missouri thinned to 60 percent stocking based on Gingrich's (1967) stocking

equation (Crunkilton *et al.* 1988). Pubanz and Lorimer (1992) reported that under two mixed hardwood shelterwoods in Wisconsin reduced to 86 percent crown cover, light intensities were 7 to 9 percent of that in the open, in contrast to 1 percent under stands not receiving shelterwood cuts. Based on the carbon budget model of Hanson and others (1987), even those modest increases in light intensity would sustain the growth of red oak seedlings. Nevertheless, the greater root growth that occurs at higher light intensities (Gottschalk 1985, Kolb and Steiner 1990) supports the case for maintaining light intensities under shelterwoods as high as practical. Marquis (1973) concluded that the practical light range for shelterwoods in Allegheny hardwoods extends upward to 60 percent of full light.

According to a study in the southern Appalachians, reducing overstory density by up to 40 percent by thinning from below can increase red oak seedling diameters up to three times that of seedlings under unthinned stands (Loftis 1990b). Similar increases in the size of oak reproduction were observed under thinned oak stands in the Boston Mountains of Arkansas (Graney and Rogerson 1985). The latter study also showed that the optimum residual stand density for the development of oak reproduction is about 60 percent stocking based on Gingrich's (1967) stocking equation. Shelterwoods thus can increase both survival and growth of oak reproduction before final overstory removal. Studies in Wisconsin also have shown that the number of red oak seedlings can be increased by shelterwood cuttings when combined with understory competition control (Pubanz and Lorimer 1992).

A prescription for applying the shelterwood method has been developed for productive sites (site index 70 to 90) in mixed stands in the southern Appalachians (Loftis 1983b, 1990a, 1990b). These stands have dense subcanopies of tolerant hardwoods that typically comprise 15 to 30 percent of total stand basal area. The prescription calls for a two-cut shelterwood in which stand basal area is reduced to 60 to 70 percent of average maximum stand basal density, depending on site index. This is accomplished by removing stems from below using an herbicide, which also prevents their sprouting. The method thus eliminates the subcanopy and thereby increases light near the forest floor without creating large gaps in the main canopy. On site indexes of 70, 80, and 90, recommended residual basal areas are 60, 65, and 70 percent of initial basal area, respectively. Reducing stand density below these limits increases the establishment of yellow-poplar seedlings to densities that are incompatible with regenerating red oak. Recommendations are to make the initial shelterwood cut at least 10 years before the end of the rotation. Applying this prescription can substantially increase the survival rate (fig. 5a) and growth of red oak seedlings. The method also is compatible with minimizing risks from oak decline because it causes minimal site disturbance and overstory canopy reduction.

A predictive model for estimating "dominance probabilities" facilitates quantitative expression of the regeneration potential of red oak reproduction under shelterwoods in the Appalachian region (Loftis 1990a). A dominance probability is the probability of an advance reproduction stem being dominant or codominant 20 years after shelterwood removal. Probabilities increase with increasing basal (groundline) diameter and decreasing site index. On site index 70, probabilities range from 0.01 for reproduction 0.1 inch in basal diameter to 0.46 for reproduction 1.6 to 2 inches in diameter; on site index 90, probabilities range from 0 to 0.34 for the same range of diameters (table 2). In application, the expected future numbers of dominant and codominant red oaks per unit area can be calculated by multiplying the observed number of seedlings in each of several basal diameter classes by the dominance probability for each class and summing those products across all diameter classes.

Although there may be 1,000 to 2,000 northern red oak seedlings per acre under red oak stands in Appalachian forests (Loftis 1983b, Tryon and Carvell 1958), the seedlings may average only 0.2 inch or less in basal diameter (Loftis 1988). If the above shelterwood prescription were applied, relations among seedling survival, growth, and dominance probabilities indicate that 1,000 well-distributed seedlings per acre should produce 10 to 40 dominant and codominant red oaks per acre 20 years after final overstory removal across the site index range of 90 to 70, respectively. Even though these estimates are hypothetical and remain to be verified by long-term field tests, they nevertheless indicate the potential for maintaining red oak as a component of regenerated stands. But success in maintaining the species largely depends on site quality, stand density, and competition control.

Table 2.—*Twentieth-year dominance probabilities*[a] *for northern red oak advance reproduction in the southern Appalachians*

Basal diameter[b] of advance reproduction (inches)	Oak site index[c]		
	70	80	90
	Probability		
0.1	0.01	0	0
0.2	0.02	0.01	0
0.3	0.04	0.02	0.01
0.4	0.06	0.03	0.01
0.5	0.09	0.04	0.02
0.6	0.13	0.06	0.03
0.7	0.17	0.09	0.04
0.8	0.21	0.12	0.06
0.9	0.25	0.15	0.08
1.0	0.29	0.18	0.11
1.1-1.5	0.38	0.29	0.19
1.6-2.0	0.46	0.41	0.34

[a]*The probability that a stem of red oak advance reproduction will be dominant or codominant 20 years after overstory removal (from Loftis 1990a).*

[b]*Measured at groundline.*

[c]*Height in feet at an index age of 50 years based on the curves of Olson (1959).*

The documented successes in applying the shelterwood method in mesic ecosystems emphasize the importance of controlling competition, including interfering herb, shrub, and tree layers (Crow 1992, Horsley 1991, Jacobs and Wray 1992, Johnson *et al.* 1989). Herbicides probably provide the most efficient method of competition control, but opposition to their use has prompted evaluation of other methods. And scarification, especially on steep terrain, may not always be feasible or environmentally acceptable.

Fire, often associated with the origin of many oak forests, also may have a place in the application of the shelterwood method (Abrams 1992, Lorimer 1985, McGee 1979). Preliminary results from prescribed burns under shelterwoods suggest that competition can be effectively reduced with two fires spaced 2 to 3 years apart (Nyland *et al.* 1982). In contrast, single low-intensity burns are not likely to be effective in controlling competition (Johnson 1974, Loftis 1988, Nyland *et al.* 1982, Will-Wolf 1991). Based on a review of literature and other considerations, Van Lear and Waldrop (1988) concluded that frequent low-intensity back fires with low flame heights would be the most useful for building up oak advance reproduction under a shelterwood. Such burns are not likely to damage the overstory or sites. In contrast, high-intensity head fires may cause excessive overstory mortality from flames that reach into tree crowns. Site damage also could result. However, even when mortality of overstory trees is avoided, fire injury can reduce the economic value of stands (Loomis 1973, Rouse 1986). Although oaks in general are relatively fire resistant because of their thick bark, the resistance of northern red oak ranks behind that of bur oak (*Q. macrocarpa* Michx.), black oak, and white oak (Lorimer 1985).

Prescribed burning nevertheless has the potential to promote the accumulation of red oak reproduction. This occurs in at least three ways by: (1) eliminating or reducing the number of fire-sensitive understory competitors, including shrubs and shade-tolerant trees; (2) reducing overstory density by killing trees with thin, fire-sensitive bark; and (3) killing back the tops of oak reproduction, which increases the root:shoot ratio and ultimately the root mass of those that survive by resprouting. The first two factors increase light on the forest floor, which in turn creates conditions more conducive to the

accumulation of oak reproduction. The third factor increases the probability of rapid height growth after overstory removal. Northern red oak is well adapted to surviving fire because of the concentration of dormant buds near the root collar. These buds often remain an inch or more below the soil surface where they are protected from lethally high temperatures (Korstian 1927).

The seed tree method

The seed tree method is an even-aged method that provides for seed production after most of the parent stand has been harvested. A typical application leaves 10 or fewer seed-producing trees per acre (Smith 1986). However, the method generally has not been recommended for regenerating oaks because the seed trees are likely to contribute too little too late to a stand's regeneration potential. In the few reported cases where the method has been applied to oak stands, the seed trees had little or no effect on regeneration (DeBell *et al.* 1968, Johnson and Krinard 1983). The method nevertheless may be useful in some ecosystems if combined with competition control, as discussed for clearcutting. It also has the potential to provide for substantial acorn production if good seed producers are retained. However, identifying seed producers requires long-term records on the acorn production of individual trees (Johnson 1993). Although the crowns of some seed trees may degenerate from crown dieback resulting from their sudden exposure (Smith 1986), the snags that ultimately develop may provide valuable cavities for wildlife and the standing dead wood essential to preserving biodiversity (Franklin *et al.* 1989, Hansen *et al.* 1991). Seed trees can be converted to dead snags by girdling, once it is determined they have little or no value for acorn production or other purposes. The method also creates more structural diversity, and to some, more visual appeal than a clearcut.

The group selection method

The group selection method is an uneven-aged system that also is potentially suitable for regenerating northern red oak. The method requires creating small openings in the main canopy to provide the conditions necessary for the establishment of new reproduction and/or the growth of advance reproduction. When single-tree selection is used to remove trees between groups, the method preserves some of the characteristics of a mature forest (Marquis and Johnson 1989). Recommended opening size ranges from one-tenth to one-half acre (Law and Lorimer 1989, Marquis 1989, Roach 1963). Larger openings should be referred to as patch cuts or clearcuts if the objective is to perpetuate these as even-aged units through successive rotations (Marquis 1989). All of the potential regeneration problems and solutions common to the clearcutting method also apply to the group selection method.

A disadvantage of the group selection method where timber quality is important is the large ratio of perimeter to opening area that results from small canopy openings. For example, ten 1/3-acre circular openings (3.3 acres) create 3.2 times more perimeter (forest edge) than a single 3.3-acre circular clearcut. Forest-grown oaks are prone to develop epicormic branches when exposed to the high light intensities occurring along forest edges, which, in turn, reduce their bole quality and value (Trimble and Seegrist 1973). However, light intensity along opening edges is a function of opening diameter and other factors (Fischer 1981, Minckler *et al.* 1973). Another disadvantage of the group selection method is the increasing difficulty of fitting new openings among older ones (Marquis and Johnson 1989).

A variation of the group selection method is the group shelterwood method (Coder *et al.* 1987, Smith 1986). In this method, groups are removed where oak advance reproduction has accumulated either by design or chance. Because oak reproduction tends to occur irregularly in time and space, the resulting groups are likely to be similarly irregular. In some cases, these patches of reproduction can be enlarged by gradually removing the overstory around their perimeter. However, a disadvantage of this procedure is that it tends to follow rather than guide the development of reproduction (Smith 1986). The method nevertheless has potential application in sustaining timber production where other values including aesthetics are important and an even flow of wood products is not critical. It is compatible with preserving diversity and aesthetics near sensitive recreation, scenic, and other areas that are not regulated for timber production. The method also can be used to remove groups of dead or dying trees impacted by gypsy moth, oak decline, or other agents. However, such salvage

cuttings may intensify crown dieback in trees that border group openings (Kessler 1992). Murphy and others (1990) concluded, based on theoretical considerations, that the proper application of the group selection method is unlikely to produce dysgenic effects. Nevertheless, the method has the potential to create such problems, as discussed below for the single tree selection method.

The single tree selection method

The single tree selection method generally is considered inappropriate for regenerating oak forests (Hibbs and Bentley 1983, Sander and Clark 1971). Canopy openings the size of individual trees generally do not provide adequate light and space for the recruitment of red oak reproduction into the overstory. The method also encourages the development of a tolerant understory of trees and shrubs, which tends to offset any regeneration advantages resulting from reduced overstory density (Auclair and Cottam 1971, Della-Bianca and Beck 1985, Loucks and Schnur 1976, Schlesinger 1976, Trimble 1970). Moreover, the method is regarded as a practice with potentially dysgenic consequences (Smith 1986, Zobel and Talbert 1984). Howe (1989) proposed that the method can avert those effects only if: (1) the defined age classes are narrow, (2) the oldest and largest trees within *each age class* are cut, (3) outstanding phenotypes in younger age classes are not cut, and (4) poor phenotypes in each age class are removed in each cutting cycle. He further emphasized that meeting the above standards essentially requires knowing the age of each tree, but questioned the practicality of determining such. Those considerations emphasize the need for careful implementation of the selection method, especially where the method is invoked in the name of biodiversity or other worthy environmental objectives.

Artificial Regeneration

Direct seeding

Results of direct seeding trials with northern red oak have ranged from unsuccessful to uncertain (Krajicek 1960, Marquis *et al.* 1976, Mignery 1975, Russell 1971, Scholz 1964, Sluder *et al.* 1961, Zaczek *et al.* 1993). A major problem has been animal predation of acorns and the lack of practical methods to prevent it. Even when direct seeding has produced acceptable initial stocking of new seedlings, subsequent survival and growth generally have not been acceptable. In contrast, direct seeding of inherently fast-growing bottomland oak species has succeeded when used in conjunction with intensive site preparation that completely removes competing vegetation and thus rodent cover (Johnson and Krinard 1985). Although direct seeding in combination with effective competition control may have potential application to regenerating northern red oak on some upland sites, planting is now the more reliable method.

Planting

Northern red oak can be successfully planted on forest sites, despite numerous reported failures (e.g., Hilt 1977, Loftis 1979, McGee and Loftis 1986). However, opportunities for planting vary by region and among the many kinds of ecosystems within regions. Probably the best opportunities occur within the site index range of about 60 to 70, where site quality meets the growth requirements of northern red oak but where competition is not too severe. Outside this site index range, it may be difficult to justify planting for ecological and economic reasons.

In this setting, planting can be used to supplement natural reproduction and thereby reduce regeneration costs by minimizing the number of planted trees needed to attain a given future stocking goal (Johnson and Rogers 1985). To that end, the reciprocals of estimated dominance probabilities of planted trees are useful expressions of the numbers of trees that must be planted to obtain one "successful" tree. Estimated dominance probabilities are available for trees planted in shelterwoods and clearcuts in the Missouri Ozarks (Johnson 1989, 1992). Because of the large number of planting trials now underway, dominance probabilities may soon be determined for other regions and regeneration schemes. Guidelines and models for evaluating the natural regeneration potential of oak stands are available for several regions and can be used to complement planting prescriptions (Loftis 1990a, Marquis *et al.* 1984, Sander *et al.* 1984, Waldrop *et al.* 1986).

Shelterwoods provide a favorable environment for the initial establishment of planted red oak seedlings. Under a shelterwood, seedlings can recover from planting shock before they encounter the surge of competition that develops after

overstory removal. For bare-root nursery stock, this recovery period is critical because the physiological disruptions resulting from lifting, handling, and planting ("planting shock") delay root elongation, and reduce leaf and root surface area the first few years after planting (Johnson 1988, Johnson *et al.* 1984, Struve and Joly 1992). Results from a Missouri study indicate that retaining the shelterwood for 3 years allows a sufficient recovery period (Johnson 1984). However, red oak can persist under shelterwoods for many years. For example, 11 years after planting, 86 percent of red oaks under thinned jack pine (*Pinus banksiana* Lamb.) stands in Ontario were still alive and 76 percent of those were vigorous stems averaging 10 feet in height (Stroempl 1987a).

Although the optimal shelterwood density for underplanting may vary among ecosystems, results from several studies indicate that some reduction in overstory density is necessary for satisfactory growth of planted trees. Residual stand densities near 60 percent stocking or 75 to 85 percent crown cover often have provided the requisite conditions (Gottschalk and Marquis 1982, Lorimer 1989, Pubanz and Lorimer 1992, Teclaw and Isebrands 1991). Even though thinning below those levels risks encouraging the growth of competitors at the expense of planted trees, one study on a drymesic site (red oak site index 61 ft) in northern Wisconsin demonstrated that 25 percent crown cover may be better than 0 or 70 percent (Teclaw and Isebrands 1993). On those sites in that northerly region, a light shelterwood may provide effective protection against late spring frosts, and yet not stimulate the competition enough to seriously impede the growth of planted trees. But in many other ecosystems, controlling low shade from shrubs, small trees, and herbaceous vegetation may be at least as important as controlling high shade (Horsley 1991, Lorimer 1989, Pubanz and Lorimer 1992, Teclaw and Isebrands 1991). Control of understory vegetation with herbicides provides the dual advantages of increasing light during the shelterwood period as well as reducing competition after shelterwood removal. The shelterwood thus should be removed as soon as possible after treatment to minimize the reestablishment of competition.

In the Missouri Ozarks, good opportunities for planting red oak under shelterwoods occur on north- and east-facing slopes, which also are where site quality is favorable for the growth of planted trees and where the regeneration potential of oak advance reproduction is most often deficient (Sander *et al.* 1984). A prescription for planting northern red oak under shelterwoods on those sites calls for: (1) controlling woody understory vegetation with an herbicide before planting, (2) thinning from below to create a shelterwood at 60 percent stocking based on Gingrich's (1967) stocking relations, (3) spring underplanting of 1+1 or undercut 2+0 nursery stock averaging at least 0.5 inches diameter (1 inch above the root collar) that have been top-pruned 6 to 8 inches above the root collar, and (4) removing the shelterwood three growing seasons after planting (Johnson *et al.* 1986). If this prescription is applied, about 60 percent of planted trees are predicted to be dominant or codominant 5 years after the shelterwood is removed (Johnson 1989).

It also may be feasible to underplant northern red oak without the use of herbicides if anticipated losses to suppression from competition are compensated by modest increases in the number of planted trees (Johnson 1992) (table 3). With or without weed control, the number of planted trees required to obtain, on the average, one future dominant or codominant tree decreases rapidly with increasing initial seedling diameter (table 3). Planting large nursery stock, although more expensive than small stock, is less costly per "successful" planted tree (Johnson 1989). Investment analysis of managing for oaks versus allowing stands to succeed to sugar maple showed that oak underplanting may be a viable economic alternative in Iowa and Missouri forests (Countryman and Miller 1989).

Red oak also can be planted in clearcuts, but dominance probabilities are lower there than under shelterwoods, other factors being equal. For example, predictive models estimate that 37 percent of 1+1 transplants 0.5 inches in initial diameter will be competitively successful 8 years after planting in Missouri clearcuts in contrast to 61 percent of those that remain under a shelterwood for 3 years (Johnson 1989). Better results were observed in a West Virginia clearcut planting where at least 50 percent of bare-root seedlings were judged successful 5 years after planting (Wendel 1980).

Table 3.—*Number of 1+1 transplants or 2+0 undercut seedlings that must be planted to obtain one dominant or codominant tree 5 years after shelterwood removal with and without herbicide treatment*

Initial shoot diameter[a] (1/16 inch)	Planted trees needed to obtain one dominant or codominant tree	
	Treated with herbicide[b]	Not treated with herbicide
	- - - - - number[c] - - - - -	
4	3.42	5.52
5	2.58	3.95
6	2.11	3.08
7	1.83	2.55
8	1.64	2.20
9	1.51	1.96
10	1.42	1.78

[a]*Measured 1 inch above the root collar.*

[b]*Based on the application of Tordon RTU[7] to cut wood understory stems ≥0.5-inches d.b.h. and to stumps of overstory trees removed in the shelterwood and final harvest cut.*

[c]*Numbers are the reciprocals of estimated planted tree dominance probabilities, i.e., probabilities of attaining dominance or codominance within 5 years of shelterwood removal. (From Johnson 1989, 1992).*

Red oak also has been successfully planted in one-twentieth and one-tenth acre openings in red pine (*Pinus resinosa* Ait.) plantations in Ontario (Stroempl 1987b). After 10 years, survival of planted trees was 98 percent, and 61 percent of those averaged 10 feet in height and were of good stem quality. Old fields also can be planted either as pure stands or in mixture with other species such as red pine (Stroempl and Beckwith 1978, von Althen 1979). Success in planting old fields, like planting on forest sites, largely depends on effective site preparation and seedling quality (von Althen 1979). However, unfavorable physical, chemical, and biological soil properties associated with abandoned farmland can hinder the growth of planted red oak (Carmean *et al.* 1976).

Unlike seedlings planted under shelterwoods, top pruning did not benefit trees planted in clearcuts in Missouri (Johnson 1989) and Pennsylvania (Zaczek *et al.* 1993), and depressed the growth of trees planted in West Virginia (Wendel 1980). The physiological cause of such differences in response to top pruning is unknown. However, for seedlings planted under shelterwoods in Missouri that were not top pruned, mortality increased with increasing seedling diameter. In contrast, mortality of top-pruned seedlings neither increased nor decreased with increasing diameter (Johnson 1988, 1989). Those relations suggest that large intact stems act as a respirational drag and a sink for the modest amounts of photosynthates produced under the low light intensities of shelterwoods (Crunkilton *et al.* 1988).

For a given initial seedling size, container-grown seedlings outperform bare-root seedlings in clearcuts but not in shelterwoods (Johnson 1984, Zaczek *et al.* 1993). The better performance of container-grown seedlings may be related to their intact roots, and the correlated after-planting advantages of rapid initiation of root and shoot growth, development of large leaf areas, and maintenance of favorable internal water status (Crunkilton *et al.* 1988, Johnson *et al.* 1984, Struve and Joly 1992). However, container-grown seedlings of the requisite size are expensive to produce, and the marginal advantages in field performance may not justify their higher cost (Johnson 1989, Zaczek *et al.* 1993).

Placing plastic tree shelters around planted red oaks can accelerate their growth (Lantagne 1991, Mintner *et al.* 1992, Teclaw and Isebrands 1991) and also protect them from animal damage such as deer and rabbit browsing. Thus, tree shelters also could be used in conjunction with direct seeding and natural regeneration.

[7]*Mention of trade names does not constitute endorsement of the products by the USDA Forest Service.*

However, the high cost of tree shelters may detract from their biological advantages. Such shelters nevertheless may make it biologically feasible to regenerate red oak on some highly productive sites and perhaps other sites that would otherwise be unfeasible to plant.

Undercutting seedlings in the nursery is a relatively inexpensive way to improve field performance. Advantages result from increased "plantable" root mass and number of large lateral roots from which new roots arise after field planting (Johnson 1988, Schultz and Thompson 1991). Schultz and Thompson (1991) recommend planting only seedlings with six or more first-order lateral roots 1 mm or larger in diameter. For trees planted in Missouri clearcuts, dominance probabilities were up to 0.12 higher for undercut than for not undercut seedlings, depending on initial seedling diameter (Johnson 1988). However, undercutting also reduces seedling growth in the nursery, which necessitates a 2-year nursery production period to realize the dual benefits of large size and increased root fibrosity. Although there is evidence that the best field performance can be obtained by planting large seedlings with numerous large lateral roots, seedling size is probably the more important factor (Kaczmarek and Pope 1993).

Reducing nursery bed density to 6 to 8 seedlings per square foot can increase the proportion of seedlings with acceptable numbers of large lateral roots while simultaneously increasing the average size of seedlings (Schultz and Thompson 1991, Teclaw and Isebrands 1991). Other factors also can affect the field performance of planted red oaks, including seed source, seed quality, nursery fertilization, irrigation, soil management, seedling lifting, and storage practices (Buchschacher *et al.* 1991, Johnson 1989, Schultz and Thompson 1991, Teclaw and Isebrands 1991, Webb and von Althen 1980).

SUMMARY

Northern red oak can be managed as even-aged or uneven-aged stands and regenerated by several silvicultural methods. Success in using a given system or method will depend on its compatibility with the dynamics of the ecosystem where it is to be applied. Although red oak occurs in moderately dry to mesic ecosystems, best growth occurs in the mesic ecosystems, which are characterized by several vegetative strata including the main tree canopy, tree subcanopy, shrub, and herbaceous layers. Where several strata are present, the species usually is restricted to one generation in the absence of disturbance or silvicultural intervention because red oak reproduction will not persist under the prevailing deep shade. Many of today's red oak stands originated during the 19th century, a period of frequent and widespread grazing and burning across much of the species' range. Those events often created conditions favorable for the establishment and growth of red oak at the expense of competitors.

Available tools for managing established stands include general management guides, growth and yield models, stocking charts and equations for controlling stand density, site index curves and predictive equations based on soil and topographic factors, and in some regions, ecological classification systems. Guidelines also are available for minimizing damage and mortality from gypsy moth defoliation, oak decline, and associated secondary organisms and effects, which are serious problems in some areas.

Timing and intensity of intermediate cuttings will depend on the natural stand dynamics of the ecosystem where they are to be applied. For example, maximizing bole quality in red oak stands in New England is facilitated by maintaining maximum stand densities rather than thinning during the first 40 years. This approach to early stand management is feasible in that region because survival and growth rates of young red oaks are high relative to those of the predominant competitors, red maple and birch. In other regions, early crop tree release may be necessary for red oak to attain and maintain dominance, especially if the competition is yellow-poplar, sugar maple, or beech. But even where competition is severe, recommendations are to defer thinning until crop trees are at least 25 feet tall. Exceptions include red oak stump sprouts, whose growth and quality can be increased by thinning clumps to one stem as early as age 5 years. To ensure bole quality, the safe lower limit for residual stand density is usually "*B*-level" stocking percent as defined by stocking charts and equations. Stands older than about 60 years should not be thinned. Rotation lengths for sawtimber range from about 80 to 120 years depending on management objectives, site quality, and other factors.

Regeneration is probably the least well understood facet of northern red oak silviculture. Regeneration uncertainties largely result from unpredictable acorn crops and thus initial establishment of seedlings. Subsequent development of reproduction largely depends on light, soil moisture, and competition relations beneath the parent stand. Adequate numbers, size, and spatial distribution of this "advance reproduction" usually are essential to regeneration success in the absence of pre- or post-harvest competition control. Unfortunately, northern red oak advance reproduction is often absent or scarce, especially in mesic ecosystems. Where advance reproduction is adequate, northern red oak can be regenerated by clearcutting or by the group selection method. If the latter method is used, group openings should be at least one-third acre. In the Driftless Area, preliminary evidence suggests that red oak can be regenerated by clearcutting even when advance reproduction is absent if the final harvest is coordinated with a good acorn crop and competition control.

Where regeneration problems occur, the shelterwood method may be the most effective solution, especially in the troublesome mesic ecosystems. In applying the method, recommendations are to reduce stand density to about 60 percent stocking or 75 to 85 percent crown cover by thinning from below. Controlling one or more components of the understory, including herbaceous species, shrubs, and undesirable advance reproduction also may be necessary, depending on their density and size. The length of the establishment period will depend on the initial status of red oak reproduction, frequency of good acorn crops, and losses of acorns and seedlings to insects, herbivory, adverse weather, and several other factors. A decade or longer may be required. Guidelines for evaluating the adequacy of oak advance reproduction and stand regeneration potential are available for several regions and can be used to monitor the development of reproduction under shelterwoods. When stand regeneration potential is deemed adequate, the shelterwood can be removed. Red oak also can be successfully planted under shelterwoods if large nursery stock is used and problematic understory vegetation is controlled. Plantings are most cost effective when they are designed to supplement a stand's natural regeneration potential.

In general, the current status of northern red oak silviculture is characterized by: (1) the predominance of even-aged management; (2) great variation in cleaning and thinning schedules, which depend on regionally variable economic and ecological constraints; (3) the failure of clearcutting, by itself, to regenerate the species in many ecosystems; (4) the potential to increase regeneration successes through application of the shelterwood and clearcutting methods when those methods are used in conjunction with competition control coordinated with acorn production; (5) difficulty in regenerating red oak on the most productive sites (i.e., site index >70); and (6) uncertainty in maintaining the species at its current range-wide level of importance because of the combined effects of regeneration failures and unknown long-term impacts of the gypsy moth and oak decline. Despite problems, current silvicultural knowledge can be used to effectively manage and successfully regenerate northern red oak in many ecosystems.

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Reviews the state-of-the-art knowledge about northern red oak shoot growth patterns, flowering, carbon allocation, and silviculture.

KEY WORDS: Ecosystem, *Quercus rubra*, flowering, shoot growth, photosynthesis, roots, shelterwoods, regeneration.

Our job at the North Central Forest Experiment Station is discovering and creating new knowledge and technology in the field of natural resources and conveying this information to the people who can use it. As a new generation of forests emerges in our region, managers are confronted with two unique challenges: (1) Dealing with the great diversity in composition, quality, and ownership of the forests, and (2) Reconciling the conflicting demands of the people who use them. Helping the forest manager meet these challenges while protecting the environment is what research at North Central is all about.